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ECOLOGY OF THE NATIVE VEGETATION OF THE LOESS HILLS IN CENTRAL NEBRASKA

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INTRODUCTION

In central Nebraska, near the eastern border of the largest grassland association in North America, there occurs a vast area of bluffs and valleys and uneroded, level uplands known as the Loess Hills and Plains. About half the region, which is several thousand square miles in extent, is still clothed with native grasses. These extensive range lands, a part of which are now under cultivation, form an important agricultural resource of the state. This area is a part of the mixed prairie association (Weaver & Clements 1938) and is represented by a comparatively large number of individual prairies which are disturbed only by annual mowing. The types of vegetation have recently been clearly delimited; there are four distinct communities in every prairie of considerable size (Weaver & Bruner 1948). The short-grass type, dominated by blue grama (*Bouteloua gracilis*),[1] was found in the drier portions of most prairies. The mid- and tall-grass type, composed principally of big bluestem (*Andropogon furcatus*) and side-oats grama (*Bouteloua curtipendula*), occurred in the ravines and on the lower slopes of the hills. A transitional type, where blue grama shared dominance with one or several of the mid and tall grasses, formed the characteristic layered vegetation of typical mixed prairie. An unusual type, where western wheat grass[2] (*Agropyron smithii*) alone dominated, was found wherever the predrought vegetation had been disturbed to such a degree that invasion and establishment became possible.

This study was made to ascertain the composition, structure, interrelationships, and environmental factors of the various plant communities. The prairies studied were on non-sandy soils in Custer, Buffalo, Sherman, and Valley counties. The field work was carried out during the summers of 1948 and 1949.

The writer wishes to express his appreciation to Dr. J. E. Weaver for suggesting this study and for his efficient guidance during the course of the work and in the presentation of the data. He is also indebted to Dr. A. P. Mazurak for his help with the soil analyses.

REVIEW OF LITERATURE

The first recognition of the mixed prairie as an association was by Clements (1920). Shantz (1923) later described the natural vegetation between the Rocky Mountains and the 98th meridian from Canada to Texas. Since then ecological studies on grasslands have become quite numerous and some of these have dealt with the climax condition.

[1] Nomenclature of grasses follows Hitchcock's "Manual of the Grasses of the U. S.," that of other species is according to Britton and Brown's "Illustrated Flora," unless other authority is given.

[2] Hereafter this species will be referred to as wheat grass.

In west-central Kansas, Albertson (1937) has studied in great detail several types of grassland in one large prairie. Bruner (1931) delimited and examined this association in Oklahoma. Weaver and Bruner (1948) made preliminary studies of the vegetation described in this paper. To the north, the relationships between soil heterogeneity and plant distribution were studied in the grasslands of North Dakota (Hanson & Whitman 1938). Considerable information is available on different portions of the mixed prairie in Canada (Clarke, Campbell, & Campbell 1942; Moss 1944). Coupland (1950) in his monograph gives a comprehensive survey of mixed prairie in Canada together with an extensive citation of the literature.

Vegetation of the sandhills, which border the loess hills on the west, has been studied by Pool (1914) and more recently by Tolstead (1942). The true prairie eastward has been studied more thoroughly than any other grassland association. Steiger (1930) made a detailed analysis of one large prairie near Lincoln, Nebraska. The most comprehensive reports over very large areas of true prairie are those by Weaver and Fitzpatrick (1932, 1934).

A three-year comparison of environmental factors in true prairie and mixed prairie was made by Clements and Weaver (1924). The environment of true prairie over a period of years has been reported by Weaver and Himmel (1931). Behavior of the grasslands during and following the great drought of 1933 to 1940 has been reported in a series of papers (Weaver & Albertson 1940, 1943, 1944; Albertson & Weaver 1942). This drought resulted in the modification or nearly complete destruction of most grassland communities in the plains states. Finally, the stabilization of the grasslands after a complete cover of grasses had been developed has been discussed by Weaver (1950).

GEOLOGY

"The area is developed principally on mantle rock materials of Pleistocene age. During middle and later Pleistocene time the interfluve areas received relatively thick mantles of wind-blown dust known as loess. Much of this was blown up from alluvial flats along the through valleys of the region. The Sandhills released much Tertiary and Pleistocene loess-forming material which contributed directly or indirectly to the Loveland and Peorian deposits. The aggregate thickness of the loess mantle approaches 150 feet or more in places.

"Headwater erosion into the loess plain has rapidly developed the characteristic canyon topography of the region. Once the sod and thin soil cap of the upland plain is removed by undercutting, the relatively coarse silts of the loess erode rapidly.

"Before the Peorian loess was deposited on it, a dark soil with a clayey subsoil was developed at the top of the Loveland loess. Water easily enters and penetrates downward through the Peorian loess often to 30 or 40 feet. At the contact with Loveland loess its further penetration is greatly restricted. Hence, the ground water movement is directed laterally toward the valley or canyon sides where water is discharged as springs and causes the overlying Peorian loess to slip or slide valleyward. Catsteps are thus developed. These are a typical feature of the side slopes of the uplands" (Weaver & Bruner 1948).

SOILS

The deep, well-developed soils of the upland are mostly of the Holdrege series (Hayes, *et al* 1928). The topsoil is dark brown in color and usually ranges from 8 to 12 inches in thickness (Fig. 1). Color becomes progressively lighter with increase in depth until the yellowish-white parent material is reached.

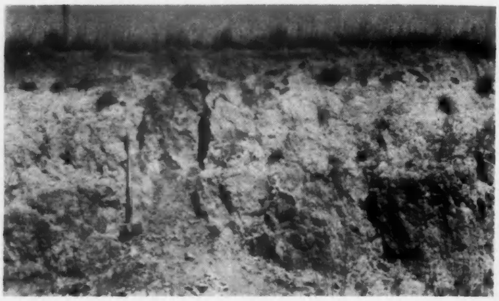

FIG. 1. Soil profile southwest of Ansley, Nebraska. Lower dark portion, which occurs here from 4 to 5 feet below the surface, is a topsoil probably of Loveland loess buried in geological time under the present lighter-colored Peorian loess.

Lime content is high and the carbonates are usually leached to a depth of 3 to 6 feet. They were found much deeper in cracks in the soil, in old root channels, and on the surface of living roots, where they were sometimes as deep as 18 feet.

The immature Colby soils are present over a large part of the uplands. Erosion prevents the accumulation of much organic matter and topsoil is thin and light in color. It ranges from 4 to 8 inches in thickness but may be much less. Since the water runs off rapidly there is no zone of lime accumulation and the surface soil rests directly on the parent material.

Approximate percentages of sand, silt, and clay were obtained by making at least 2 determinations of each composite sample by means of the hydrometer method (Bouyoucos 1936). Silt content was never less than 50 percent and was usually considerably higher (Table 1). This with lack of cementation causes the soil to erode rapidly when the protective cover of vegetation is removed. The maximum total sand content was 20 percent and in some places there was less than 15 percent at certain depths. Most of this was very fine sand and no gravel or coarse sand was present. Clay content was usually between 20 and 30 percent. In a normal profile it was greatest at a depth of 6 to 18 inches. The soils were mostly in the silt loam textural classification.

TABLE 1. Results of mechanical analyses of soils from the three major plant communities.

Depth in feet	SHORT GRASS			MIXED GRASS			MID AND TALL GRASS		
	Sand >0.05 mm.	Silt 0.05 to 0.002 mm.	Clay <0.002 mm.	Sand >0.05 mm.	Silt 0.05 to 0.002 mm.	Clay <0.002 mm.	Sand >0.05 mm.	Silt 0.05 to 0.002 mm.	Clay <0.002 mm.
0-.5...	12.3	60.0	27.7	18.0	53.7	28.3	15.0	57.5	27.5
.5-1...	9.3	50.0	39.7	16.9	52.9	30.2	15.7	55.7	28.6
1-2...	10.9	54.4	34.7	19.2	52.7	28.1	15.4	57.4	27.2
2-3...	14.0	65.6	20.4	20.0	53.8	26.2	17.9	53.4	28.7
3-4...	14.4	63.3	22.3	15.5	61.5	23.0	14.4	55.7	29.9
4-5...	16.0	61.8	22.2	15.5	59.5	25.0	15.0	55.7	29.3
5-6...	17.1	59.8	23.1	13.0	64.8	22.2	19.8	55.6	24.6
6-7...	16.9	61.9	21.2	13.2	60.8	26.0	19.1	55.8	25.1
7-8...	16.8	58.0	25.2	12.2	64.1	23.7	17.1	57.6	25.3

Moisture equivalents of the soils were obtained by rotating saturated samples in a centrifuge at a rate equal to 1000 times gravity for a period of 40 minutes (Briggs & McLane 1910). Hygroscopic coefficients were obtained by the method described by Alway, Kline, and McDole (1917). These data are shown in Table 2. The hygroscopic coefficient is considered as the amount of water in the soil which is unavailable for plant growth.

TABLE 2. Moisture equivalent (M.E.) and hygroscopic coefficient (H.C.) of 27 soil samples taken at the various depths in each of the principal types of vegetation.

Depth in feet	SHORT GRASS		MIXED GRASS		MID AND TALL GRASS	
	M.E.	H.C.	M.E.	H.C.	M.E.	H.C.
0-.5......	26.43	10.61	27.89	10.72	27.26	9.44
.5-1......	30.44	13.58	27.62	10.66	27.20	9.42
1-2......	28.50	12.34	24.45	9.45	25.72	9.09
2-3......	24.98	9.89	24.29	9.17	24.19	8.69
3-4......	23.08	9.13	23.97	8.70	23.72	8.67
4-5......	23.34	9.01	23.93	8.86	23.59	9.48
5-6......	22.82	9.12	23.32	8.50	20.14	7.63
6-7......	22.34	8.51	24.23	8.98	21.23	7.81
7-8......	22.98	8.56	23.56	8.69	20.92	7.86

Total nitrogen was determined by the modified Gunning method and percentage organic matter by the modified Walkley-Black method. These determinations were made on the surface 4 inches of soil only. Least amounts of nitrogen and organic matter were found in the mixed-grass type on the hillsides where large amounts of soil have been removed by erosion. Greatest amounts were found on a level hilltop under a dense growth of short grasses (Table 3).

TABLE 3. Average percentage of nitrogen and organic matter in the surface 4 inches of soil in the principal communities as determined from numerous samples.

Communities	Nitrogen	Organic matter
Short grass..........	0.283	5.12
Mixed grass..........	0.183	3.58
Mid and tall grass.....	0.218	4.58

ENVIRONMENT

The altitude ranges from approximately 1,900 to 2,450 feet above sea level. Dissection of the upland plain has resulted in a terrain which is rolling to extremely hilly (Fig. 2). In the southern and eastern portions the hills are lower and the slopes more gradual than nearer the sandhills westward. Level areas of considerable extent are seldom found. They occur principally on the plain near the center of the divides where dissection has not yet taken place.

FIG. 2. General view of a typical prairie showing the characteristic rolling terrain.

The climate is of the typical central Great Plains type with cold winters and hot summers. The average growing season is about 148 days. Annual precipitation, most of which falls during the growing season, averages 23.3 inches, but it is somewhat greater in the eastern portion of the area. The average maximum for the year occurs during June when approximately 4 inches is received. A large part of the rain falls in local thundershowers resulting in uneven distribution. Stations separated by only a few miles occasionally receive amounts differing by an inch or more. About 26 inches of snow falls during the winter and when accompanied by wind, as frequently occurs, it tends to accumulate in the ravines. Wind movement is often high during the summer and relative humidity is usually low.

A station was selected in each of several communities where environmental factors were measured. The short-grass station was located on a hilltop with a slight southwest exposure; the mixed-grass station was on an east slope with protection from the west only; the mid- and tall-grass station was in a broad level ravine protected from the west and to some extent from the east; the wheat grass station was located at the base of a long slope facing southwest; the shrub-thicket station was in a pocket on an east-facing bank. The greatest distance between any two stations did not exceed 500 feet.

TEMPERATURE AND HUMIDITY

Air temperature was recorded once or twice weekly at each station. Readings were taken at a height of 3 inches above the soil surface. They were made at all stations within a period of 15 minutes at about

TABLE 4. Average of various environmental factors in 5 habitats between June 5 and August 8, 1948. The range of each factor is given below the average. Measurements of temperature and relative humidity were taken weekly at about 2 P. M.

Community	Air temp. F°	SOIL TEMPERATURE F°			Relative humidity percent	Vapor pressure deficit in. Hg.	Avg. daily water loss c.c.	Avg. daily wind movement m.p.h.
		Surface of soil	3″ below surface	6″ below surface				
Shrub thicket	83.3 (71–89)	76.5 (75–84)	71.5 (64–74)	67.0 (63–73)	51.5 (47–60)	.560 (.38–.74)	10.1 (4–20)	....
Mid and tall grass	83.1 (71–92)	87.8 (81–96)	75.5 (72–80)	71.0 (65–78)	56.8 (45–76)	.483 (.31–.70)	6.5 (2–10)	0.77 (.3–3.5)
Mixed grass	86.1 (72–93)	97.0 (81–108)	78.7 (72–84)	75.3 (68–79)	47.2 (37–54)	.657 (.37–.91)	19.1 (9–30)	3.01 (2.4–8.1)
Short grass	88.3 (76–95)	102.0 (83–112)	81.3 (78–90)	76.3 (73–83)	44.2 (35–51)	.724 (.42–1.00)	23.8 (10–37)	4.23 (2.6–13.1)
Wheat grass	88.3 (76–95)	102.7 (83–114)	85.3 (80–94)	78.4 (74–85)	42.5 (33–50)	.748 (.33–1.07)	....	....

2 P.M. The relative mesophytism of the various plant communities is indicated by their arrangement in Table 4, where the most mesic is placed first. There was usually a difference in temperature of 3° to 6° F. between the lowland stations and those of the more exposed ones. Temperature variations were never great on the lowland between the mid- and tall-grass station and the shrub thicket. Likewise temperatures on the upland were somewhat similar in the short-grass community and wheat grass type. It would seem that air temperature had little or no effect on the distribution of these communities (Weaver & Himmel 1931).

Soil temperatures were obtained immediately after the air temperatures were taken. The surface temperature was obtained by placing the bulb of the thermometer in a horizontal position about 1 millimeter beneath the soil surface, or on the soil under the plant debris where it was present. It was also recorded at depths of 3 and 6 inches and occasionally at 3 feet.

The surface temperature in the shrub thicket was lowest. It averaged 26.2° F. less than that at the wheat grass station where the temperature was highest. Even at a depth of 6 inches there was a difference of 11.4° between these stations. Temperatures in the mid- and tall-grass community were lower at all soil depths than at the short-grass station. Differences of 14.2°, 5.8°, and 5.3° occurred at the surface, 3 inches, and 6 inches in depth, respectively. As is usual, the amount of variation in temperatures between the different stations decreased at greater depth in the soil. The greatest decrease in temperature from the surface to a depth of 6 inches was found under wheat grass where surface temperatures were the highest. By the middle of June the soil temperature in the mixed-grass type at a depth of 3 feet had reached 61° and by the middle of August it was 73°. At a depth of 6 feet the temperature was 10° less than at 3 feet during July.

The insulating value of a mulch was shown by the marked increase in temperatures where the mulch was thin or absent. Even in the same habitat, differences as great as 10° were found under various thicknesses of mulch. Here as in the true prairie (Weaver 1942), the soil surface in the wheat grass type was almost without a mulch.

The cog psychrometer was operated at a height of 3 inches above the soil surface each week at the time the temperatures were obtained. These data were used to determine both relative humidity and vapor pressure deficit. The latter averaged .483 inches at the mid- and tall-grass station, and was greater at each of the other stations (Table 4). It was very much greater at the wheat grass station (.748 inches) than in the lowland where the tall grasses were growing. Relative humidity likewise indicated that the air was driest at the wheat grass station.

EVAPORATION

Livingston's, standardized, white, spherical atmometers, each with a non-absorbing device, were operated during 1948 at each station except the one in the wheat grass. The bulb was placed 3 inches above the soil surface. The average daily loss of water in cubic centimeters per week is shown in Figure 3. The high rate of evaporation at the short-grass and mixed-grass stations is an excellent indicator of weather conditions during the two-month period from late June to late August. The low rate of evaporation from the middle of July until the middle of August was caused by cool, moist weather. The actual evaporating power of the air in each of the habitats is probably best illustrated very early in the season before the moderating effect of the vegetation becomes a factor. The marked effect of the mid- and tall-grass community in decreasing evaporation first became clearly evident during the second week of July (Fig. 3). As the vegetation in this community increased in height and density, there was a decrease in loss of water from the atmometers. At each of the other stations where height and den-

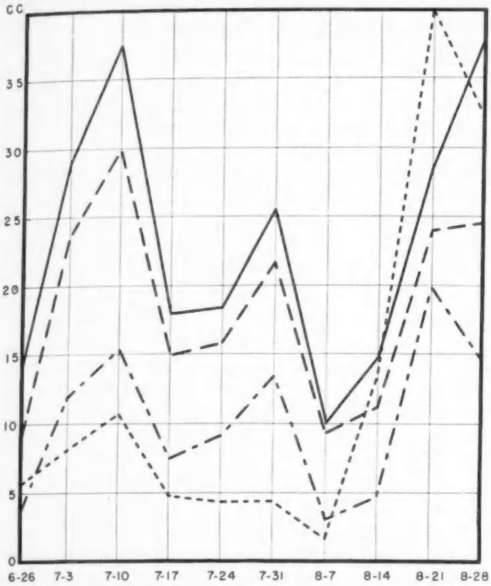

FIG. 3. Average daily evaporation in cubic centimeters in the communities of short grass (heavy unbroken line), mixed grass (long broken lines), mid and tall grass (short broken lines), and shrub thicket (alternate long and short lines). Averages are for the weeks ending on June 26 (6-26), etc., during 1948.

sity of the vegetation were less than in lowland, fluctuations in the amount lost were more marked.

During most of the summer, evaporation was greater in the shrub thicket than in the mid- and tall-grass type. Very little sunlight penetrated the upper layer of the shrubs and consequently the lower layer was poorly developed. This permitted rather free movement of air and more evaporation than would otherwise have been possible. As the tall grasses increased in stature, they not only furnished almost complete shade but also effectively decreased movement of air currents. As a result, dew or other moisture remained on the leaves until near the middle of the day a large part of the time. Mowing of the lowland vegetation during the second week of August resulted in a marked increase in evaporation (Fig. 3). Water loss was even greater than that at the more xeric types where continued growth of vegetation was causing a reduction in evaporation.

Increased loss at the short-grass station during the last week of August was probably due to more or less constant warm southwest winds. The average daily loss at this station in weekly periods exceeded 30 cubic centimeters only twice during the season and was less than 20 cubic centimeters 50 percent of the time. Evaporation during the entire season averaged 266 percent greater at the short-grass station than at the mid- and tall-grass station.

WIND

Four-cup anemometers were operated at a height of one-half meter on the hilltop, hillside, and lowland in plant communities characteristic of these habitats. Plants in the immediate vicinity of the anemometers were repeatedly clipped in order to avoid interference with the movement of the cups. The relative rates of wind movement in the various communities corresponded in a general way with the rates of evaporation (Fig. 4). The steady decrease in rate in the mid- and tall-grass type as the season progressed was directly related to the increase in the height of vegetation. A similar decrease at the other stations began later in the season due to the slower increase in height of the vegetation on the uplands. Wind movement on the hilltop in the short-grass type had an average rate through the season of 1.22 miles per hour greater than on the east slope in the mixed-grass type (Table 4). Effect of vegetation on wind movement at the height of the anemometers is well illustrated by the increased rate after the vegetation on the lowland was mowed.

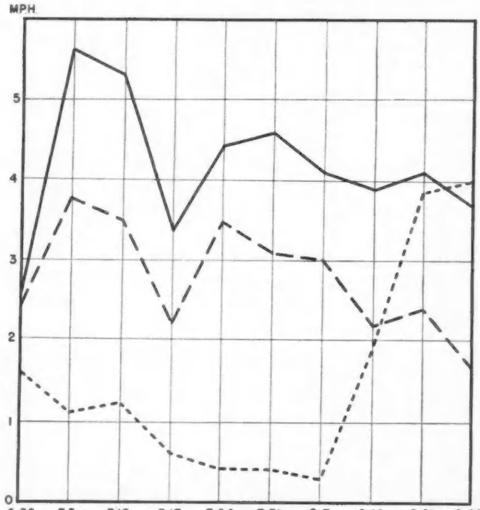

FIG. 4. Average weekly wind movement in miles per hour in the communities of short grass (heavy unbroken line), mixed grass (long broken lines), and mid and tall grass (short broken lines). Averages are for the weeks ending on June 26 (6-26), etc., during 1948.

Before mowing, the average wind movement was only .77 mile per hour, while after mowing it increased to an average rate of 4 miles per hour. This occurred despite a decrease in wind movement at the other stations during the same period.

PRECIPITATION

Rainfall records were obtained from the Soil Conservation Service in Broken Bow and from a private gauge maintained 10 miles south of this station. The precipitation reported here is the average from these stations. April and May, 1948, were very dry. The total rainfall was 4.8 inches below normal. During the next two months 4.7 inches more than the normal precipitation were received. Total rainfall for the

growing season was only about an inch below normal. The excess rainfall during the summer did not offset the droughty conditions of spring and the vegetation was somewhat dwarfed. It is apparent that good seasonal distribution of this moderate rainfall is of great importance, as is also a sufficient amount to thoroughly wet the soil.

Rainfall during the following growing season was below normal every month except June, when there was .75 inch more than normal. Total deficit for the 5-month period was nearly 4 inches. However, distribution was more favorable and the grasses developed normally. Drought during July caused the vegetation to become almost entirely dependent on subsoil moisture.

SOIL MOISTURE

Soil samples were taken weekly, by means of a Brigg's geotome in each type of vegetation. In order to ascertain the amount of moisture present, the samples were weighed and placed in an oven at a temperature of 105° C. for 24 hours. Samples of the first and second 6-inch soil layers were taken separately, but all others to a depth of 6 or 8 feet were taken in cores one foot in length. Soils in 8 habitats in 2 prairies were sampled in 1948 and in 4 habitats in a single prairie the following year. The short-grass type from which samples were taken was located on a level hilltop; the mixed-grass type was on a west-facing hillside with a slope of approximately 5 percent; the mid- and tall-grass type was in a broad level ravine; the wheat grass type was at the base of a long north-facing slope; the catsteps were on a steep ravine bank. All moisture in excess of the hygroscopic coefficient was considered to be available for plant use. Moisture in the surface foot of soil correlated closely with current rainfall, but at greater depths fluctuations were more gradual. Surface moisture was rapidly depleted during extended dry periods.

The soil below a depth of 1 foot in the short-grass type never had as much as 10 percent available moisture until near the end of the season. This maintained despite heavy rainfall during the summer months of 1948. Usually there was less than 5 percent to a depth of 4 feet. In still deeper soil there was from 5 to 8 percent present throughout the season (Fig. 5). The slow rate of growth of the short grasses after the middle of July, together with their shorter roots, which never extended deeper than 7 feet, permitted the conservation of more of the soil moisture than where more deeply rooted, mid and tall grasses were growing.

There was ordinarily less soil moisture present on the hillsides, where runoff is greater. However, the amount of runoff water would depend on several factors, including the nature of the rainfall, the degree of slope, and the amount of cover. The deeply rooted mid and tall grasses require more moisture over a longer period of time than do the short grasses. As a result, at the end of the season the soil moisture in the mixed-grass type was more nearly exhausted than where only short grasses were dominant.

Decrease in soil moisture on the hillsides was further shown by its increase in the lowlands (Fig. 5). More than 10 percent available moisture was present in the upper 3 feet of soil during the last half of July and during August. Moisture from current rainfall and run-in water never extended deeper than 4 feet and there was a gradual decrease in moisture throughout the season below this depth. The rapid rate of growth of the tall grasses during August resulted in a large amount of water being removed from the soil.

The soil was always driest where wheat grass was the dominant species, regardless of the site in which it grew. There was seldom more than 2 percent available moisture present except in the upper foot of soil (Fig. 6). From 3 to 4 percent was available

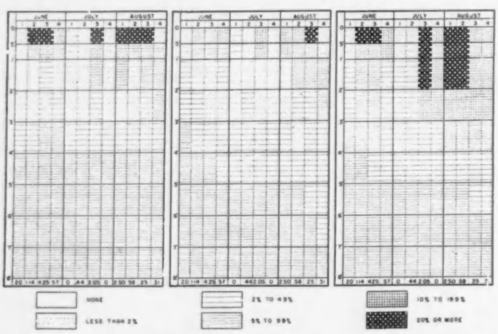

FIG. 5. Available soil moisture by weeks in 1948 to a depth of 8 feet in the several communities: short grass (left), mixed grass (middle), and mid and tall grass (right). The numbers at the foot of each column show the amount of rainfall received each week.

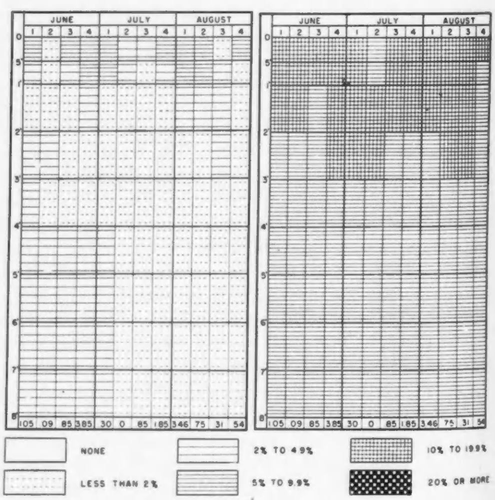

FIG. 6. Available soil moisture by weeks in 1948 to a depth of 8 feet in the wheat grass type at the base of a long slope (left) and on a catstep where tall grasses were growing (right). The numbers at the foot of each column show the amount of rainfall received each week.

during the early part of the season at depths of 4 to 8 feet, but this was largely depleted by the first week of July. Continued drying of the soil after this time did not occur since wheat grass had completed most of its growth. These data illustrate the fact that wheat grass not only uses an excess of water but also retards the normal rate of infiltration under prairie grasses (Weaver & Albertson 1943). The low basal area and almost complete absence of a mulch are not conducive to absorption of water by the soil.

An entirely different situation was found on the steep catsteps where there was a rank growth of vegetation, consisting mostly of tall grasses. Here water infiltrates rapidly into the soil, as is clearly shown in Figure 6. There was always less than 20 percent available moisture since percolation is rapid, but more than 10 percent was available in the upper 3 feet of soil throughout most of the season. Only on two occasions was there less than 15 percent available moisture in the top 6 inches of soil. The heavy accumulation of mulch aided infiltration and effectively prevented evaporation from the soil surface. Vegetation was rank and considerable moisture must have been used in transpiration. Nevertheless, the soil contained more than 5 percent available moisture at 3 to 8 feet in depth during the entire season.

Distribution of rainfall in 1949 differed considerably from that of the previous year, and this resulted in definite differences in the pattern of soil moisture. All moisture used the previous season had been replenished during winter and spring. Amounts of available moisture in the short-grass and mixed-grass types were somewhat similar. Little rain fell after the second week in June, and the surface moisture rapidly became exhausted. The distribution of rainfall in August was such that it did little toward replenishing soil moisture lost during the early summer. Exhaustion of moisture at 4 to 6 feet in depth followed the same pattern as during 1948.

In the mid- and tall-grass community in the lowland, the first 2 feet of soil was nearly saturated during the first 3 weeks of June. More than 10 percent available moisture was present in the subsoil most of the season. Not until late August did the roots decrease the moisture supply to less than 10 percent below a depth of 4 feet. The soil in the wheat grass type was even drier than in 1948. Below a depth of 2 feet almost no moisture was available for plant growth throughout the season.

METHODS OF STUDYING VEGETATION

Thirty prairies were studied in varying degrees of intensity throughout the growing seasons of 1948 and 1949. They ranged in size from less than 20 to more than 300 acres; several consisted of 100 acres or more. Most of the quantitative data were taken from the larger tracts since here the environment was less affected by surrounding ranges and cultivated fields. Summer grazing was never practiced, but grazing in winter was not uncommon. Some ranchers merely raked the hay into windrows, after it was mowed in late August or September, and left it for the cattle to consume in winter.

An intensive study of small samples of vegetation in the various types was made in a total of 300, square-meter quadrats. Each quadrat was divided into units of either 4 or 10 square decimeters. These small areas permitted an accurate estimate of the total basal area furnished by the vegetation. Basal area as used here refers to the percent of soil surface covered by vegetation at a height of one inch. It is the horizontal area occupied by the bunch or mat of vegetation at this height. The percent of the total vegetation which each of the grasses furnished was also ascertained. In estimating the percentage of vegetation any one species composed, the total basal area of all vegetation present, whether it was small or large was considered as 100 percent. Thus, one small patch of blue grama might comprise 100 percent of the vegetation in one plot, but the same sized patch might constitute only 10 percent where the cover was dense. All the forbs were grouped together since they ordinarily contributed but little to basal cover. The vegetation in 50 quadrats, most of which were in the short-grass type, was charted by means of a pantograph. A planimeter was used to measure the basal area recorded on the pantograph charts. These quadrats not only revealed the composition and basal area of the vegetation but also furnish a permanent record of its distribution at the time they were made.

Several transects were made in each of the typical prairies. They extended completely across the prairie at right angles to the ravines. The width of each of the several communities, which alternated and recurred again and again, was measured by the number of paces required to cross it. When a large number (about 40) of these transects were made, the average distances traveled in each community were compiled in order to ascertain the approximate percent of each type of vegetation in the prairies studied. Circular sample areas, each including 50 square feet, were laid out in the several communities. The number varied with the size of the community. A record was made of the number of forbs of each species occurring within each circle. The number of stems of some species was counted rather than the number of plants, since many species were of a rhizomatous nature and individual plants were difficult to distinguish.

Ecotones on representative hillsides were studied by use of transects a decimeter wide. The transect was divided into units 2 decimeters long, and the grasses in each unit were recorded in their order of abundance. The trench method of investigating root systems (Weaver 1926) was used to study the underground parts of 1 to 3 individuals of each of the 25 most important species of grasses and forbs. The trenches were made in roadside banks in order to facilitate the removal of soil. Root systems were sketched as they were exposed. At the end of each growing season, 100, square-meter quadrats were

clipped in order to determine forage production. Short grasses, mid and tall grasses, and forbs were clipped and air dried separately. They were then weighed to the nearest tenth of a gram. Each week notes were made on the height and condition of vegetation, including the production of flower stalks and inflorescences.

PLANT COMMUNITIES

The four principal communities or types of vegetation were found in every prairie of considerable size. The short-grass and mixed-grass types were of approximately equal extent in the entire area; each covered an average of about 33 percent of all the prairie areas. The mid- and tall-grass type comprised approximately 27 percent of the area, while the wheat grass type and shrub thickets made up the remaining 7 percent. However, there was considerable variation in the amount of each type in the individual prairies.

A total of 164 species of plants were found in the prairie area. These included 27 perennial grasses, 3 annual grasses, 4 sedges, and 113 forbs. In addition, 11 shrubs and lianas and 6 trees commonly formed postclimax vegetation in certain lowlands. Sedges of infrequent occurrence were not counted, and certain rare species were probably overlooked.

SHORT-GRASS TYPE

Typically the short-grass faciation occurred on the hilltops and extended some distance down the hillsides. The distance depended somewhat on the exposure and slope and whether or not catsteps were present. On south and west exposures this community often continued to the base of the hill. But when the hilltop abruptly gave way to a north or northeast slope, this type was usually replaced by more mesic vegetation. This faciation never occurred in the ravines, on catsteps, or on steep banks. Despite the fact that this was a widespread community, it was almost entirely absent in some prairies. Frequently small tracts with a topography too rough for farming were left in native vegetation, but they rarely supported the short-grass community. The steep, rough land was more suitable for taller grasses, which are able to inhabit less stable soils. In other prairies the open cover of short grasses had been invaded by wheat grass resulting in the formation of the mixed-grass type. It is likely that here, as in other parts of the mixed prairie, death of many of the mid grasses had resulted in a great increase in area occupied by the short grasses. Large areas of the mixed prairie association, according to Weaver and Albertson (1940), were converted to a short-grass disclimax by the drought.

GRASS AND SEDGES

As the name indicates, the short-grass type is characterized by the dominance of short grasses. In fact, two short-grass species, blue grama and buffalo grass (*Buchloe dactyloides*), were the only dominant grasses, although a few weedy grasses composed some of the vegetation. Blue grama was the chief xeric dominant. It alone furnished 90.9 percent of the vegetation and occurred in every quadrat sampled (Table 5). Sometimes it was found in pure stands but more frequently it was intermixed with a small amount of other grasses, sedges, and forbs. Even though short rhizomes are present at the base of the culms, blue grama exhibits a bunch habit in these prairies and rarely forms a sod. Tillering is rapid when moisture is abundant. It may become dormant at any time during the growing season and renew growth soon after a rain. This is a chief reason why this grass is a dominant here. Furthermore, it can produce seed at any time from June to early September if conditions are favorable. Blue grama is the most drought resistant of all the native grasses of mixed prairie (Mueller & Weaver 1942). In both true prairie and mixed prairie, it often survived where all other grasses succumbed to drought. Scattered spikes were produced through most of the summer of 1948, but not abundantly until after the middle of August. Height of foliage was seldom more than 4 to 5 inches, but flower stalks were 6 to 18 inches tall. In some prairies there was considerable blue grama with pilose leaves. These were distinguished only with difficulty from those of buffalo grass. Hairy leaves of blue grama had been noticed on individual plants elsewhere, but they had never been so abundant. The well branched roots extended to a depth of about 6.5 feet. Their lateral spread was sufficient to thoroughly occupy most of the soil between the plants.

Buffalo grass furnished considerable basal area where it was present, but its distribution throughout the community was quite erratic. It composed only 4.7 percent of the vegetation and was present in 42 percent of the quadrats (Table 5). It was of most importance where the soil was somewhat compacted and therefore was found in greatest abundance near

TABLE 5. Percentage composition and frequency of occurrence of the most important grasses in each community. Data on other grasses and forbs are also given. Average basal area in each type is shown.

Species	Short Grass		Mixed Grass		Mid and Tall Grass		Wheat Grass	
	Comp.	Freq.	Comp.	Freq.	Comp.	Freq.	Comp.	Freq.
Bouteloua gracilis	90.9	100	49.5	100	0.3	8	4.0	35
Agropyron smithii	0.5	50	4.0	64	2.2	52	75.9	100
Andropogon furcatus	...	..	8.4	48	56.0	90	...	..
Carex spp.	1.1	80	6.8	97	10.6	88	10.9	67
Bouteloua curtipendula	...	..	17.7	83	13.2	62	0.9	29
Sporobolus cryptandrus	0.4	31	4.2	64	1.0	18	6.0	52
Poa pratensis	...	..	0.2	5	7.9	34	...	..
Buchloe dactyloides	4.7	42	1.3	16	...	..	...	..
Koeleria cristata	0.7	33	2.1	57	0.9	38	0.7	8
Muhlenbergia cuspidata	0.4	10	1.8	40	1.4	15	...	..
Panicum wilcoxianum	0.4	18	1.3	38	0.5	22	...	..
Artistida purpurea	...	..	1.2	20	0.4	11	0.4	11
Other grasses	0.1	..	0.5	..	3.4	..	0.9	..
Forbs	0.8	92	1.0	99	2.2	83	0.3	41
Basal area	31.1		18.7		8.8		3.5	

roads and trails. Occasionally it grew in pure stands in isolated areas throughout the community. It is not so drought resistant as blue grama, but spreads much more rapidly than this species when growing conditions are favorable. Stolons have been observed to reclaim bared areas in silty clay loam soils by growing at the rate of an inch per day for several days in succession (Albertson 1937). New roots develop from the nodes and penetrate the soil if the surface is moist. The roots are very fine and similar in nature and extent to those of blue grama. It is much more deeply rooted than are the sedges which are nearly always more or less abundant in short grass.

Carex pennsylvanica and *C. eleocharis* were considered together since they are difficult to separate vegetatively and are ecologically similar. They grow in small tufts that seldom exceed 4 inches in height and contribute very little either to basal cover or to forage production. They occurred in 80 percent of the quadrats but composed only 1.1 percent of the vegetation. The sedges increased following the death of the grasses. Their presence in considerable abundance was almost certainly a result of the drought. In one prairie, *C. pennsylvanica* occurred in almost pure stands in local patches several square feet in extent. The roots were relatively shallow and reached a depth of about 2.5 feet. Lack of depth was compensated for by numerous fine branches in the surface soil. Long, tough rhizomes connected the plants and also produced occasional roots.

A number of mid and tall grasses, primarily found in other types of grassland, occurred here only sparingly. Wheat grass was the most abundant and was present in half of the quadrats. June grass (*Koeleria cristata*) was second in abundance. Both are cool-season grasses. In the dry spring of 1948, they were so greatly dwarfed in stature that in midsummer they appeared as an understory to the flower stalks of blue grama.

Hairy chess (*Bromus commutatus*) was the chief weedy, annual grass. It occasionally grew in dense stands, which almost obscured the short grasses. The great overtopping layer of this annual in 1946-47, as described by Weaver and Bruner (1948), was now thinly scattered and abundant only locally. Selective clipping of this species at the time of maturity in 1948 showed that its average yield was only 10 to 25 pounds per acre. It was greatly dwarfed because of low water content of soil in both fall and spring. Some of the plants seeded at a height of only 3 inches. In 1949 a height of 6 to 10 inches was attained, but the stand was thin and the yield was only 140 pounds per acre. This thinning of the stand of hairy chess was evidence of progress in restoration of the cover of short grass from drought damage. *Hordeum pusillum*, which occurred widely in mixed prairie elsewhere (Albertson 1937), was seldom encountered, but *Festuca octoflora* was common. The annual grasses contributed little to basal area, although they were of some importance in adding annually to the surface mulch.

BASAL AREA AND MULCH

The basal area, which was quite uniform, averaged 31 percent. It seldom exceeded 40 percent and rarely was less than 20 percent. Greatest basal area occurred where the short grasses were intermixed or where buffalo grass occurred in a pure stand. Even then it was never more than 75 percent. That it was still below normal and not yet completely reestablished was shown by occasional, large, open spaces. This is illustrated in Figure 7. Quite in contrast to the smaller interspaces, which are normally covered with a dead mulch, the larger ones were almost bare.

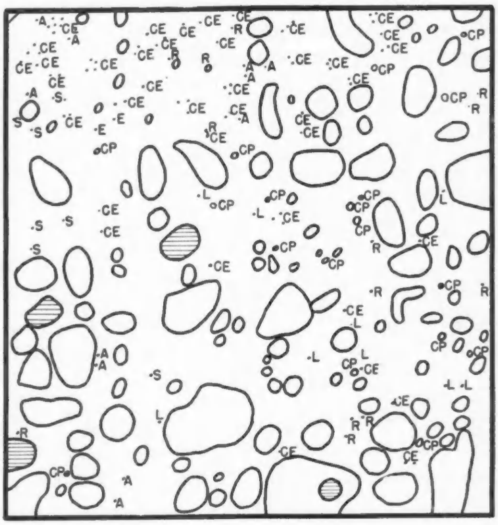

FIG. 7. Typical meter quadrat in the short-grass type showing the open cover. Total basal area is only 29 percent. Blue grama (unmarked enclosed areas) alone composes 95 percent of the vegetation. Other species are *Koeleria cristata* (horizontal lines); *Carex pennsylvanica* (CP); *Carex eleocharis* (CE); *Agropyron smithii* (A); *Lygodesmia juncea* (L); *Ratibida columnaris* (R); *Solidago glaberrima* (S); *Echinacea angustifolia* (E). Annual grasses are not shown.

The mulch, which included all dead and decaying plant remains, was present on the surface of the soil in this community in greater amounts than in any other type. Accumulation of plant material during the several years before it finally disappeared amounted to 1,743 pounds air-dry weight per acre. This occurred despite annual mowing at a height of about 2.5 inches. At Hays, Kansas, during the growing season of 1947, blue grama produced approximately 40 percent of its growth below 2.5 inches (Launchbaugh 1948). This is not removed as hay but remains on the soil as a mulch. It accounts in part for the high content of organic matter in the surface soil as well as the comparatively high rate of infiltration. Forbs, which will be considered next, add but little to this protective cover on the soil.

FORBS

Lygodesmia juncea was the most abundant forb in the short-grass community. Often there were 2 or 3 plants per square foot. Its general distribution is indicated by its occurrence in every 50-square-foot sample. This forb, like all others, was greatly reduced in numbers during the drought but was one of the few that never completely disappeared (Weaver & Albertson 1944). It is probable that the small, scale-like leaves transpire very little water, and the great depth of the roots has enabled it to be independent of fluctuating surface moisture. The slender taproot of one plant was traced to a depth of 21 feet. Near the surface it had a diameter of 13 millimeters which decreased so gradually that at 15 feet it was still 2 millimeters thick. Several long laterals but very few short ones occurred (Fig. 8).

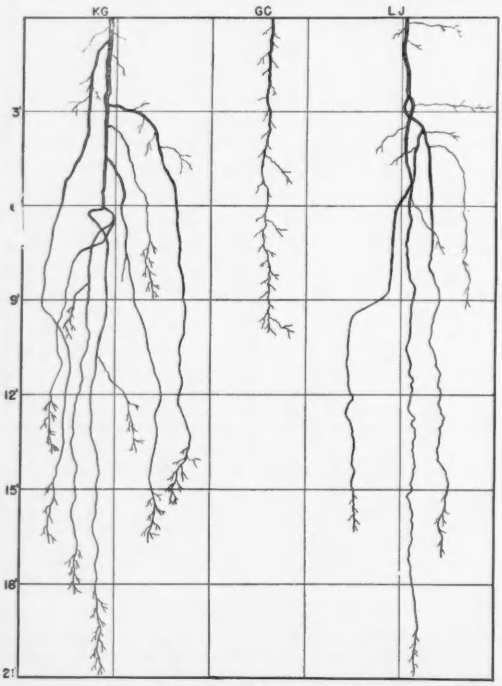

FIG. 8. Root systems of *Kuhnia glutinosa* (KG), *Gaura coccinea* (GC), and *Lygodesmia juncea* (LJ).

Ratibida columnaris was present in every prairie studied and in all but 30 percent of the sample areas. It occurred as scattered individual plants as well as in dense societies which covered entire hillsides. Here there were as many as 300 plants in a 50-square-foot sample. These dense societies were always accompanied by a small basal area of perennial grasses. This is one of the forbs which was unable to withstand the drought and consequently completely disappeared from the cover. After the soil became continuously moist, it reappeared in great numbers from seeds which had lain dormant in the soil for many years (Weaver & Albertson 1944). The roots were poorly branched and extended into the soil only 5 to 6 feet. Thus, they are forced to compete with those of the grasses, and the plants can thrive only during good years. *Ratibida columnaris* is not a stable component of the prairie but rather a short-lived perennial which fluctuates in numbers with changing condition.

Malvastrum coccineum was abundant only in this type and even here it occurred in only 25 percent of the samples. It is a small plant seldom more than 4 inches tall. It is very resistant to drought and is usually found under xeric conditions. During the drought this was the only generally distributed, native, non-grassy species, aside from cactus, that increased in mixed prairie. Later, as more mesic conditions returned, it decreased in numbers and regained more nearly its predrought abundance (Weaver & Albertson 1944). The single taproot grew almost vertically downward to a depth of 13 feet. Branching was negligible and only scattered short laterals were present throughout most of its length. The diameter of the root decreased gradually from a maximum of 4 millimeters to 1 millimeter at a depth of 8 feet. This size was maintained to a point about 1 foot from the tip of the root. At a depth of 12.5 feet the taproot entered a crack filled with deposits of lime and iron where it grew horizontally for 12 inches before again turning downward.

Other important forbs, discussed under the communities in which they are most abundant, include *Amorpha canescens, Erigeron ramosus, Psoralea tenuiflora, Gaura coccinea, Aster multiflorus*, and *Solidago glaberrima*.

LAYERING AND ASPECTS

Layering is a common expression of the structure of vegetation. Although grasses are of most importance, forbs also contribute to the various layers. There were three layers commonly found in the short-grass type. Where taller, more mesic grasses occurred, they formed a more or less discontinuous layer above the short grasses. Some wheat grass was present in about half of the short-grass community. It was dwarfed in 1948 and seldom exceeded 10 inches in height, but growth was more nearly normal the following year and the average height was 18 inches. June grass never grew in pure stands but always as thinly scattered plants; however, the distribution was so general that it occurred in 33 percent of the quadrats. In some prairies, especially where drought damage had been severe and there was an open cover of short grasses, sand dropseed (*Sporobolus cryptandrus*) formed an upper layer. Often blue grama suppressed the more mesic grasses and this layer consisted of forbs only.

The Psoralea, Ratibida, and Amorpha were the most conspicuous forbs and were commonly from 18 to 24 inches tall. *Lygodesmia juncea* was 12 to 15 inches tall. This was about the height of blue grama when it was in flower. In addition to blue grama in its

vegetative stage and buffalo grass, the lower layer contained *Carex pennsylvanica, C. eleocharis, Malvastrum coccineum, Asclepias pumila, Gaura coccinea,* and others. *Oxalis violacea* L., *Draba caroliniana, Hedeoma hispida,* and *Plantago purshii* are all short-stemmed plants which were present for a short time early in the summer.

Layering was well defined below the soil surface. Roots of most of the grasses were confined to the upper 7 feet of soil while those of June grass and the sedges were mostly in the surface 2 feet. *Ratibida columnaris, Sideranthus spinulosus, Aster multiflorus,* and *Gaura coccinea* extended their roots from 5 to 10 feet into the soil. In the lower layer, from 12 to 20 feet below the soil surface, were found the roots of *Kuhnia glutinosa, Lygodesmia juncea, Psoralea tenuiflora, Amorpha canescens,* and *Malvastrum coccineum.* Forbs not only played a part in layering but they also formed distinct societies characteristic of the four seasonal aspects.

Only a few species flowered in the prevernal aspect of late March and April and these were all low-growing plants. *Carex pennsylvanica, Anemone caroliniana,* and *Astragalus crassicarpus* Nutt. blossomed at this time. The two most important cool-season grasses, June grass and wheat grass, produced considerable foliage by the first of May.

The vernal aspect was poorly developed in 1948 due to the dry season, and signs of drought were numerous. The leaves of blue grama were rolled and those of *Erigeron ramosus* were conspicuously wilted. A general view appeared like the brown aspect of fall rather than the normal green one of spring; however, a more typical aspect prevailed during 1949. Plants flowering at this time included *Oxytropis lamberti, Lathyrus ornatus, Malvastrum coccineum, Meriolix serrulata, Psoralea esculenta,* and *Astragalus missouriensis.*

The early part of the estival aspect was similar to the vernal in 1948 in that few flowers were present, but it became better developed as precipitation increased. It was not until after the middle of June that a uniformly green aspect was present over the prairies. June grass flowered at a height of 6 inches which was conspicuously short when compared with the previous year's dead stems which were approximately 20 inches tall. *Erigeron ramosus, Ratibida columnaris, Amorpha canescens,* and *Psoralea argophylla* formed definite societies (Fig. 9). *Psoralea tenuiflora, Echinacea angustifolia,* and *Lygodesmia juncea* were also in bloom. Most of the flowers of the estival aspect were well past their prime by the early part of July. From the middle of July until the middle of August the prairie was conspicuously lacking in flowers.

Societies were more prominent in the autumnal aspect than in any previous one. *Kuhnia glutinosa* commonly grew as scattered individuals but it was sometimes found in dense patches. Societies were also formed by *Aster multiflorus, Solidago mollis, S. glaberrima,* and *Artemisia gnaphalodes. Liatris punctata* Hook. made a colorful addition to the landscape, but it always occurred as sparsely scattered individuals.

MIXED-GRASS TYPE

The mixed-grass community usually consists of a mixture of mid and short grasses and, since the drought, the tall big bluestem. This is the typical expression of the association (Fig. 10). A second community, probably formed during the drought, consists almost entirely of wheat grass and blue grama. The mixed-grass community was normally located on the hillsides where the short grasses from the hilltop mingled with the mid and tall grasses from the lowland. Occasionally it extended completely over the lower hilltops, and it was sometimes found in the lowland on knolls and in other comparatively dry areas. It was present on catsteps only when they were on the more gentle slopes.

GRASSES AND SEDGES

Blue grama composed 49.5 percent of the total vegetation and was here again the most important

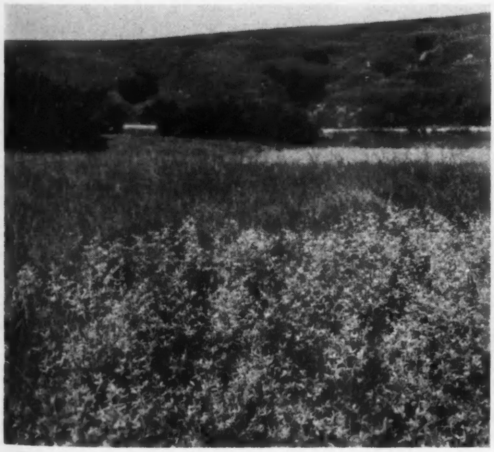

FIG. 9. Portions of two societies of *Psoralea argophylla.*

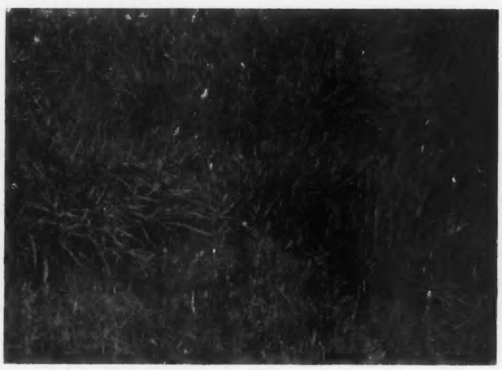

FIG. 10. Detail of a mixed-grass community with big bluestem and blue grama sharing dominance. Photo in August, 1948.

component of the community (Table 5). Sometimes it occurred in almost pure stands in small patches which alternated with areas dominated by mid and tall grasses. More frequently it was intermixed with one to several tall grasses where it occurred as an understory. It was sometimes found sharing dominance with any one of the mid and tall grasses with all others largely excluded. Individual plants in pure stands of blue grama on the hillsides were usually larger and more robust than the plants in the short-grass type. This may be correlated with the more open cover and more mesic conditions associated with the mixed-grass type. All grasses which occurred in this type were also of some importance in other communities.

Side-oats grama formed 17.7 percent of the total basal area and was the most important mid grass. Its wide distribution throughout the community is indicated by its presence in 83 percent of the quadrats. Side-oats grama produces large quantities of seed and invades new areas readily. It has increased its area at the expense of less drought resistant species in both true prairie and mixed prairie. In many prairies the increase coincided with that of wheat grass and as a result these two species became dominant over large areas. Side-oats grama was best able to compete with wheat grass when a dry spring was followed by a moist early summer (Weaver & Albertson 1944). It seems almost certain that it has also increased in the loess hills as a result of the drought. The root systems of several plants were examined. Many roots grew more or less vertically downward while others grew obliquely as far as 1.5 feet before turning downward. Well branched roots were found to extend below a depth of 8 feet. Despite numerous short rhizomes, a bunch habit of growth was usually assumed. Most of the growth of this grass, as well as the other warm-season grasses, was completed soon after the middle of August.

Sand dropseed was of rather wide occurrence and commonly grew as an overstory to blue grama (Fig. 11). It was present in 64 percent of the quadrats, but it was quite variable in amount and seemed to reach its greatest abundance where disturbance from drought was most evident. It is noted for the production of large quantities of very small seeds, which were spread widely during the drought and accompanying dust storms. Rabbits are also effective agents in disseminating the seed (Riegel 1942; Brown 1947). Sand dropseed does not compete well with the short grasses and it will probably be replaced to a large extent by other species. The roots were found to extend 9 feet below the surface of the soil.

FIG. 11. Mixed-grass type with sand dropseed as the upper layer. Photo northeast of Hazard in August, 1948.

June grass and Wilcox's panic grass (*Panicum wilcoxianum*) furnished only a small portion of the basal area, but they were rather widespread in distribution. The roots of June grass were less extensive than those of any of the other grasses and no root was ever found deeper than 2.5 feet.

C. pennsylvanica and *C. eleocharis* were of more importance here than in the short-grass type. They were present in 97 percent of the quadrats and furnished 6.8 percent of the vegetation.

Big bluestem was the only tall grass commonly found in this community, and it is probably more abundant now than formerly. It withstands drought comparatively well, and after the drought it undoubtedly spread rapidly into the recently bared areas. It made up 8.4 percent of the vegetation and occurred in about half of the quadrats sampled. The exceptionally well developed root system occupied the soil to a depth of more than 10 feet.

The wheat grass-blue grama type of mixed prairie often occurred over large areas. This community has been recently enlarged by the invasion of wheat grass into open stands of blue grama. Approximately 15 percent of the mixed-grass type had only these two species as dominants. Wheat grass composed only about 15 percent of the vegetation and is able to share dominance only by thoroughly occupying the soil with roots and rhizomes. The rhizomes grow rapidly and invade new areas readily. Even where it has only partial control, wheat grass prevents invasion by most other species by early use of water and adverse effect on the soil. Despite the fact that blue grama composed nearly 70 percent of the vegetation, the basal area was no greater than in the typical mixed-grass type.

BASAL AREA AND MULCH

Average basal area was 18.7 percent and in only one quadrat was it greater than 27 percent. It was highest wherever blue grama was most abundant. A meter quadrat in typical mixed prairie is shown in Figure 12, and one in the wheat grass-blue grama community in Figure 13.

The low basal area and comparatively small amount of short grasses were not conducive to the formation of a good mulch. There were only 993 pounds per acres on the surface of the soil. This was only a little more than half as much as that in the short-grass type. The greater production of mid and tall grasses above the height at which mowing takes place also reduced the amount of vegetation left to form a mulch. Bare soil was quite common in the larger spaces between plants.

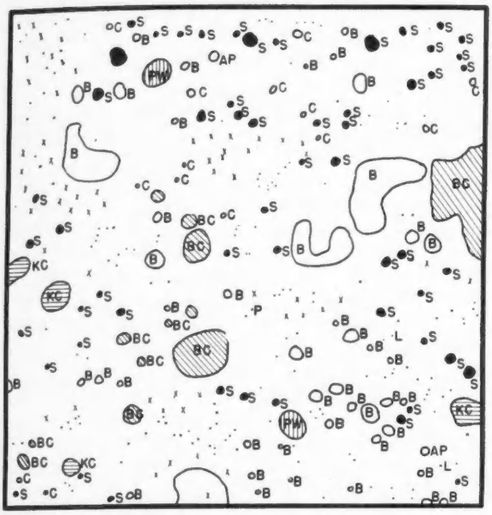

FIG. 12. Typical meter quadrat in the mixed-grass type. The basal area is about 14 percent. Blue grama (B), side-oats grama (BC), and sand dropseed (S), furnish 37.5, 32.6, and 13.0 percent of the vegetation, respectively. The remainder is composed of *Koeleria cristata* (KC), *Panicum wilcoxianum* (PW), *Aristida purpurea* (AP), *Carex pennsylvanica* (C), *Carex eleocharis* (dot), *Agropyron smithii* (x), *Lygodesmia juncea* (L), and *Psoralea tenuiflora* (P).

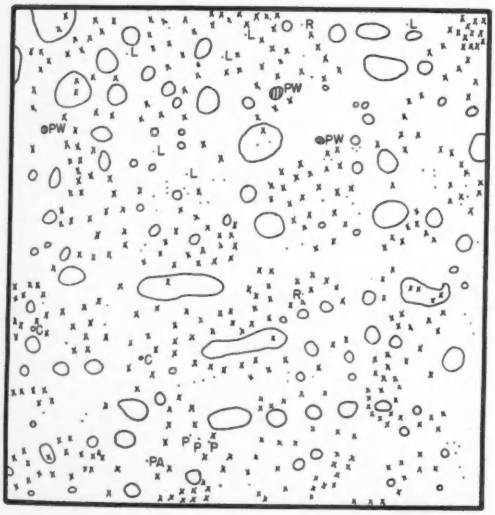

FIG. 13. Meter quadrat in the mixed-grass type where dominance is shared by blue grama (enclosed areas) and wheat grass (x). The basal area is only 10 percent. Over 90 percent of the total vegetation is blue grama. Other species are *Carex eleocharis* (dot), *Carex pennsylvanica* (C), *Panicum wilcoxianum* (PW), *Lygodesmia juncea* (L), *Psoralea tenuiflora* (P), *Ratibida columnaris* (R), *and Psoralea argophylla* (PA).

FORBS

More species of forbs were present in the mixed-grass community than in any of the others. *Lygodesmia juncea* was again the most abundant, although there were only about 33 percent as many as in the short-grass type. This species was present in greater numbers wherever blue grama or buffalo grass was abundant in the mixed-grass type. *Erigeron ramosus, Amorpha canescens, Ratibida columnaris, Psoralea tenuiflora*, and *Aster multiflorus* were usually more abundant than in the short-grass type, and together with the Lygodesmia, made up the bulk of the forb population.

Amorpha canescens is a half-shrub which behaves as a forb when mowed annually. Due to its size, widespread occurrence, yield of palatable forage, and local density, it was the most important forb in the prairie. It occurred both as scattered plants and as dense, extensive societies. As many as 70 stems were occasionally present in a sample. A specimen growing near the top of a hill extended its taproot 13.5 feet into the soil. The 5 main lateral roots were all well branched and formed a rather extensive absorbing system (Fig. 14). The taproot had a maximum diameter of 18 millimeters. This decreased to 1 millimeter at a depth of 8 feet and remained about this size almost to the tip of the root. The largest branch roots were 8 millimeters in diameter near their point of origin.

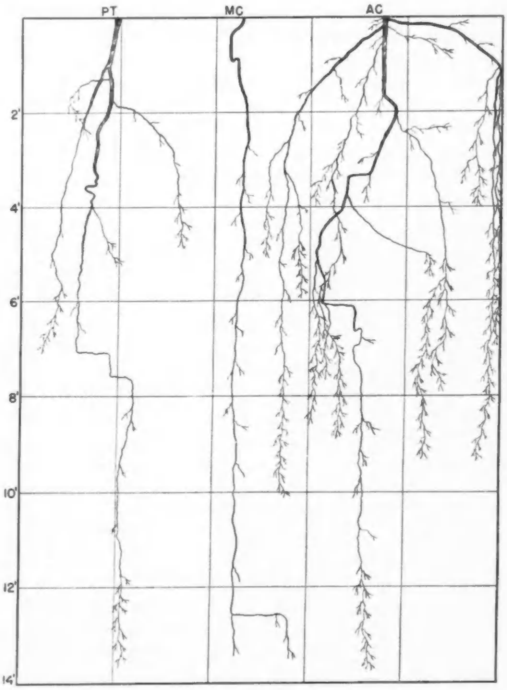

FIG. 14. Root systems of three important forbs. *Psoralea tenuiflora* (PT) *and Amorpha canescens* (AC) are distributed widely while *Malvastrum coccineum* (MC) occurs only in the short-grass and mixed-grass types.

The population of *Erigeron ramosus* fluctuates considerably from year to year. It was present in less than half the sample areas but was usually quite abundant where present. The plants grew more thickly in societies than any other plants (Fig. 15).

FIG. 15. Societies of *Erigeron ramosus* in the mixed-grass type. Photo in June, 1949.

Where Erigeron was found in great abundance, the basal area of the grasses was low. The presence of these societies is undoubtedly a result and not a cause of the low basal area. In one particular prairie there was an average of 5 plants per square foot over an entire hillside. The rosettes of this winter annual grow rapidly during the fall and produce flower stalks the following season. The roots are shallow and the leaves wilt rapidly when subjected to drought.

Psoralea tenuiflora was an important component of the prairie. It was rather uniformly distributed and the large bushy top often made it appear far more abundant than it really was. There were seldom more than 10 plants in a sample, and the average was less than 5. Abscission layers were formed near the soil surface in late summer and the presence of this leguminous form was indicated only by the dead plants tumbling across the prairie or lodged in depressions. It was thinned greatly during the drought and served as the best example of increase from seed that had lain on or in the soil for 7 or more years (Weaver & Albertson 1944). New plants appear early in the season from the strong taproot. The stem grows upward several inches before the leafy branches are expanded. When fully grown they are commonly 30 inches tall but may attain a height of 40 inches in more mesic sites. The widely spreading branches produce considerable shade, but it is of such short duration in any one place that there is no apparent effect on the grasses. Roots were traced to a depth of 13.5 feet (Fig. 14). The diameter of the taproot was 17 millimeters just below the soil surface, but it rapidly decreased in size until it was only 4 millimeters thick at a depth of 5 feet. This was probably a young plant as another previously excavated reached a depth of 15 feet and had diameter of 1.5 inches near the soil surface (Weaver & Bruner 1948).

Gaura coccinea was a small, inconspicuous plant which was sometimes present in great abundance. The taproot was shallow and poorly developed and the foliage produced very little shade.

Aster multiflorus was not of widespread occurrence but locally it grew in dense societies, where it caused a considerable reduction in the cover of grasses. The long, creeping rhizomes rapidly entered partially bared areas where they soon became well established (Mueller 1941). It had an especially well-developed root system, which penetrated the soil to a depth of 7 feet. Many fibrous roots originated from the crown, from rhizomes, and from the upper part of the taproot. These roots not only occupied the upper portion of the soil, but some were much more extensive. One branch root had a total length of over 6 feet (Fig. 16). Emerging from the base of one plant were at least a dozen, white, tough rhizomes, some of which were over a foot long. Competition with the grasses was severe both above and below ground.

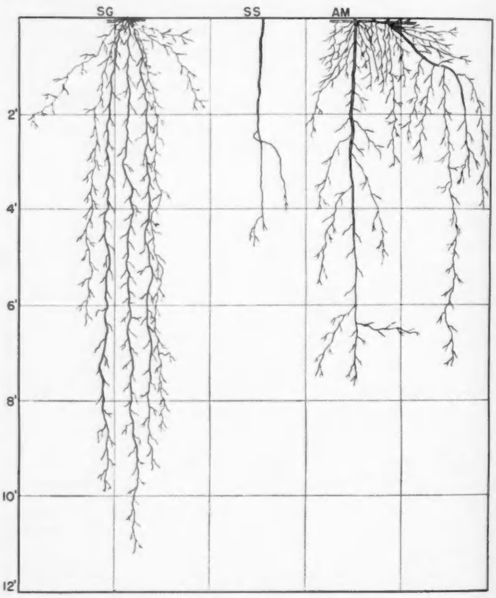

FIG. 16. Roots of *Solidago glaberrima* (SG) and *Aster multiflorus* (AM). These were important secondary species in every major community. Their generalized root systems undoubtedly furnish much competition with the dominants. *Sideranthus spinulosus* (SS) is not an abundant forb.

Solidago glaberrima also propagates by rhizomes, but the societies were seldom sufficiently dense to have other than a local effect on the grasses. The plants examined had 1 to 3 main roots, each with rather numerous short branches throughout their length of 9 to 11 feet (Fig. 16). The roots were light in color and very tough. Their diameter was never greater than 1.5 millimeters.

Astragalus plattensis Nutt. and *A. crassicarpus*

were very abundant in one prairie. There were sometimes as many as 3 to 5 plants of the latter in a 50-square-foot sample and its spreading stems covered more than half the area. The importance of this prostrate legume was not in its numbers but in the total area which it occupied. One large plant with 60 stems covered an area of 12 square feet and excluded approximately 60 percent of the normal grass cover. By the last of August the plants had dried and disappeared leaving only the fruit and large spots almost devoid of vegetation. *A. plattensis* differed in that roots emerged from the prostrate stems and many individual plants were formed. These plants also prevented the grasses from forming a normal cover.

Kuhnia glutinosa was of more importance in the mixed-grass type than elsewhere. Plants usually occurred singly, but where societies were formed, the rank growth and spreading branches competed for light with the grasses in the immediate vicinity. The taproot of one specimen, which had a maximum diameter of 20 millimeters, extended to a depth of 21 feet and produced 5 major lateral roots, some of which were rebranched several times (Fig. 8).

Forbs increase total plant production by utilizing moisture and nutrients below the roots of the grasses. Several forbs are detrimental to the grasses. *Onosmodium occidentale,* for example, occurred as single plants, but the large coarse stems often became decumbent with age and killed the grasses in the immediate vicinity. Such bare spots, some as large as 4 square feet, have been observed. Competitive effects of forbs and grasses both above and below the surface of the soil depend on the relative abundance of the forbs and on their manner of growth. Any forbs, either with or without rhizomes, which grew in societies, caused some reduction in yield of the perennial grasses. This reduction is usually compensated for by the yield of forbs, even though they may be of lower palatability. For example, in a series of quadrats in a society of velvety goldenrod, the average air-dry weight of grass was 1,228 pounds per acre and that of goldenrod was 863 pounds. This was a total yield of 2,091 pounds. In the check quadrats with few or no forbs, the total average yield was only 1,753 pounds per acre, and nearly all was palatable grass. Where lead plant occurred in considerable abundance, it reduced the yield of grasses by approximately one-third. However, this loss was more than made up by the production of its high-grade forage. On some hillsides as much as 1,500 pounds of this legume per acre was produced.

LAYERING AND ASPECTS

Layering above ground was well developed. Big bluestem, which was approximately 3 to 4 feet tall, overtopped all other species. Side-oats grama, wheat grass, and sand dropseed were 18 to 30 inches in height and constituted the most important grasses of the middle layer. Forbs present in this layer included *Amorpha canescens, Psoralea tenuiflora, P. argophylla, Kuhnia glutinosa, Erigeron ramosus, Ratibida columnaris,* and *Solidago glaberrima.* The lower layer was composed principally of blue grama, sedges, and Wilcox's panic grass. *Gaura coccinea, Solidago mollis,* and *Malvastrum coccineum* were the most important forbs in this layer.

The effects of underground layering on soil moisture were most marked in this type. June grass, Wilcox's panic grass, and the sedges were very shallowly rooted. The short grasses extended their roots to a depth of 6 to 7 feet, but the mid grasses were usually 8 to 10 feet in depth. The lower depths were occupied by roots of the same forbs as those in the short-grass type.

Species of the various aspects were similar to those of the short-grass type. However, the more mesic conditions have resulted in greater stature, more flowers, and denser societies. *Amorpha canescens,* for example, usually occurred as scattered plants on the hilltops but often in dense societies on the hillsides. *Aster multiflorus* was also more abundant. Greatest difference in aspects between the mixed-grass and short-grass types was in the autumnal aspect. The presence of late fruiting grasses in greater abundance furnished a definite contrast to the earlier maturing short grasses.

MID- AND TALL-GRASS TYPE

This community is a postclimax associes typical of the more mesic habitats. It was found wherever there was enough protection from sun and wind and sufficient available soil moisture to enable the tall grasses to largely eliminate the short grasses. It occurred on the steep banks of ravines, on catsteps, on well-protected north and east hillsides, and in most lowlands. It was best developed in the broad flat lowlands commonly called "hay pockets" (Fig. 17).

FIG. 17. Broad flat ravine (hay pocket) where the mid- and tall-grass community is best developed. Kentucky bluegrass grows vigorously following the removal of the upper layer of big bluestem and switchgrass. Photo in mid-August, 1948.

GRASSES AND SEDGES

Big bluestem, the most important grass in this type, composed 56 percent of the vegetation and was present in 90 percent of the quadrats (Table 5). It sometimes grew in pure stands, especially on the steep banks of ravines where the supply of soil moisture was always adequate (Fig. 18). It always developed a continuous sod with individual stems widely separated. Nevertheless, the dense network of roots and large, coarse rhizomes almost completely

occupied the soil. The deep root system enabled this grass to utilize moisture unavailable to plants with shorter roots. Thus, in both true and mixed prairie the amount of this grass increased after the death of its former associate, little bluestem (*Andropogon scoparius*). At present little bluestem is scarce in the loess hills and only rarely is it found as a dominant.

FIG. 18. Pure stand of big bluestem growing on a steep bank of a ravine. Photo south of Ansley in August, 1948.

A small amount of Indian grass (*Sorghastrum nutans*), wild rye (*Elymus canadensis*), and switchgrass (*Panicum virgatum*) was sometimes intermixed with big bluestem. These three grasses were found only where there was an abundance of soil moisture. Switchgrass often entirely replaced big bluestem and grew in pure stands where soil moisture approached the saturation point for considerable periods of time. This condition was common near the borders of shrub thickets. In some ravines big bluestem and switchgrass grew in a mixed stand. Slough grass (*Spartina pectinata*) was never found in the loess hills, except near the rivers which cross the area. Rapid drainage prevented the accumulation of sufficient moisture to support this hydrophyte.

The second most important grass was side-oats grama. It occasionally grew in a pure stand but more often it was intermixed with other grasses. It competed poorly with big bluestem but frequently shared dominance with wheat grass. This was especially true along the edges of ravines where there was less soil moisture than elsewhere in the lowland.

Kentucky bluegrass (*Poa pratensis*) was usually an important component of the vegetation in the lowland, where it occurred as an understory. It grew rapidly early in spring before competition was furnished by the taller grasses and again in autumn after they were mowed. Lowlands, which had a distinctly brown cast after being mowed about the middle of August, soon became green due to the vigorous growth of Kentucky bluegrass. It is apparent that here, as in true prairie, mowing has helped this European invader to become established. In all other communities the presence of this cool-season grass usually indicated a disturbance.

Wheat grass was widely distributed in this type as elsewhere. It entirely replaced the tall grasses where they had been weakened by soil deposition or other disturbance. Like Kentucky bluegrass, a large part of its growth was completed before much competition was furnished by the tall grasses.

More species of grasses were found in this type than in any other, but many of them were of limited importance. *Panicum scribnerianum* was present in 43 percent of the quadrats, yet it furnished only 0.4 percent of the vegetation. In addition to the upland sedges, the taller-growing *Carex gravida* and *C. festucacea* were present. In some lowlands the sedges furnished as much as 50 percent of the vegetation. Their distribution was erratic. They were present in moderately dry places as well as moist ones. Short grasses were rarely found.

BASAL AREA AND MULCH

Basal area was 15 percent or more where there was considerable side-oats grama or Kentucky bluegrass, but the average was 8.8 percent. Where big bluestem was present in a nearly pure stand, as on the unmowed catsteps and steep banks of ravines, it was as low as 2 percent.

The amount of mulch on the unmowed banks depended somewhat on the exposure. It was sometimes 12 inches thick, but usually less on south- and west-facing slopes. This heavy layer of debris greatly retarded early spring growth. Removal of this mulch in the spring resulted in an increase in basal area by the following autumn of at least threefold. Yield was affected very little if any. Total mulch had an average air-dry weight of over 15,000 pounds per acre, and as much as 19,000 pounds was present where conditions permitted the best development of vegetation (Dyksterhuis & Schmutz 1947). This represented an accumulation of the growth of several seasons; that added each of the last three years could be readily distinguished. The surface of the soil was always moist beneath the mulch even in the driest weather.

Where the prairie was mowed annually there was an average of only 838 pounds of mulch on the soil surface. The tall grasses produce only a relatively small amount of their total yield below the 2.5-inch height at which they are mowed. Therefore this mulch is only the stubble together with leaves and stems left in the operations of making hay.

The stability of catsteps and steep ravines is very great in contrast to that of similar areas under grazing (Branson 1951). Vegetation is usually established even on the vertical sides of catsteps. Erosion is prevented by the rank growth of vegetation and the mulch. The latter is an effective agent in promoting infiltration of water, in preventing runoff and in lessening evaporation. The loss of soil by the action of wind and water is never a problem unless the vegetation has been seriously disturbed.

FORBS

Since *Amorpha canescens* produced a large amount of palatable forage, it was considered the most important forb in the loess hills. It attained its greatest population in this type, where no other forb even approached it in abundance. It was most plentiful on hillsides and banks of ravines where dense societies were often formed, but it was never present in great numbers on lowland.

Psoralea tenuiflora was the most uniformly distributed of all the forbs in all the plant communities. It occurred here in its usual abundance (Fig. 19).

FIG. 19. *Psoralea tenuiflora* growing in the mid- and tall-grass type on a north-facing slope. Several bunches of *Stipa spartea* occur in the foreground (right), but most of the vegetation is little bluestem.

The plant becomes quite woody with age and is of little value as forage. However, it has usually broken off and been blown away by the time mowing takes place.

Other forbs were of less importance. *Symphoricarpos occidentalis* is similar to *Amorpha canescens* and *Rosa pratincola* in that it is a shrub which behaves as a forb when it is mowed annually. It was often quite abundant in the lowlands but formed societies only on the steep hillsides which were not mowed. *Erigeron ramosus, Aster multiflorus,* and *Lygodesmia juncea* were also abundant locally. *Toxicodendron rydbergii,* which is not ordinarily considered a forb, was nearly always present under the shrubs and also extended into the mid- and tall-grass type as an understory. Occasionally it was present on the hillsides where conditions permitted the growth of more mesic vegetation.

LAYERING AND ASPECTS

The tall grasses, which were 4 to 6 feet in height, furnished the upper layer. The mid grasses and such forbs as *Amorpha canescens, Psoralea tenuiflora, Rosa pratincola,* and *Symphoricarpos occidentalis* formed the middle layer, which was 2 to 3 feet in height. The lower layer was composed of Kentucky bluegrass, panic grasses, sedges, and various forbs including *Antennaria campestris, Oxalis stricta* L., and *O. violacea.*

The Antennaria formed rosettes on the surface of the soil. It was conspicuous only as it occurred in societies and produced flowers in the prevernal aspect while most plants were still dormant. *Oxalis violacea* was an important species of the vernal aspect. In 1949 it was so thick over all the prairie that it was virtually impossible to walk without stepping upon it.

The estival aspect was conspicuous due to societies of *Amorpha canescens, Symphoricarpos occidentalis* and *Rosa pratincola.* Where *Symphoricarpos occidentalis* was not mowed it often formed dense societies which almost completely eliminated the grasses. Banks of the ravines were a blaze of color due to the abundant flowers of *Rosa pratincola.* Later the forbs of the middle layer were concealed by the developing grasses.

In the autumnal aspect the fruiting grasses contributed the most color to the landscape and stood well above most of the forbs. *Solidago altissima,* however, was present in dense, colorful societies in the ravines adjacent to or among the shrubs.

WESTERN WHEAT GRASS TYPE

This consociation composed as much as 35 percent of the total vegetation in several prairies, but in others it was entirely absent. It is a product of the drought and was not confined to any particular habitat. It has appeared wherever the usual vegetation has died or has become open enough in cover to allow invasion and establishment. Areas near cultivated fields, where deposits from wind and water erosion have killed or thinned the other grasses, were often dominated by wheat grass. A pure stand was commonly found where haystacks had been located or where roads had been made though the prairie. This community was frequently found at the base of long slopes, where it ranged in width from 2 to 50 or more feet.

Wheat grass has increased tremendously since the drought in true prairie and in other parts of mixed prairie. It has undoubtedly followed the same trend here. It was an important component of every type, but where it formed a community of its own, it largely excluded other species (Fig. 20). The roots and rhizomes so thoroughly occupied the soil that in most of the type this species was in actual control of at least 95 percent of the area. The extensive roots, which reached a depth greater than any of the other grasses, penetrated the soil approximately 12 feet. Invading rhizomes from the perimeter of the community could often be followed by the development of a row of shoots. Other species within the type were always dwarfed and during dry weather they wilted much sooner than did the same species in other types. Studies in true prairie revealed that competition of wheat grass had reduced the number of species to 56 percent of those remaining in bluestem prairie and the number of stems to approximately 20 percent (Weaver 1942).

Sedges, sand dropseed, and blue grama were the most abundant species occurring with wheat grass. They always had a relatively high basal area, which made them seem more abundant than they actually were.

Average basal area in the wheat grass type was 3.5 percent, but where wheat grass only occurred the

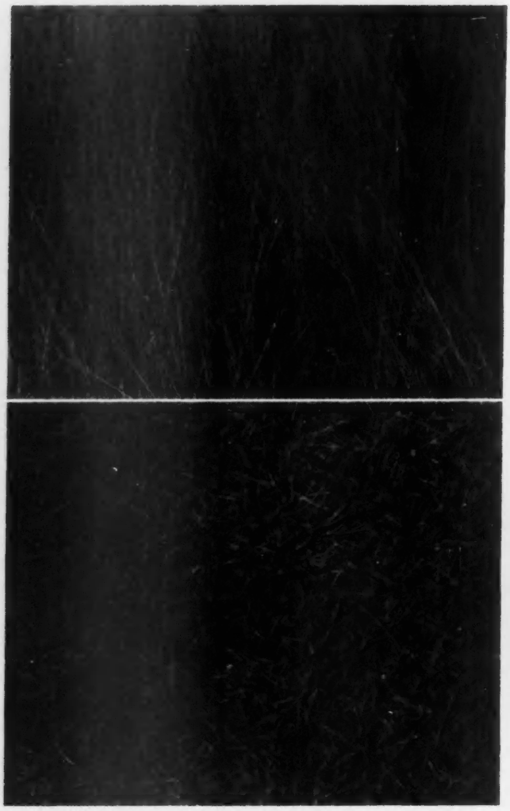

FIG. 20. Detailed view of wheat grass before and after mowing. Note the almost total absence of other species and the large amount of soil exposed.

actual area covered was usually less than 2 percent. An average of only about 700 stems was present per quadrat. There was less than 350 pounds of mulch per acre. This, with the extremely small amount of soil covered by living vegetation, resulted in a poor structure of the soil surface which retarded the germination of seeds and growth of seedlings.

Forbs were always few in number and often entirely absent. *Lygodesmia juncea* was again the most abundant, and only 4 other species were found in the entire lot of samples. Complete utilization of moisture by the wheat grass early in the season was undoubtedly a major factor in preventing the establishment of most other plants. Many of the forbs in this type were probably present before the invasion of wheat grass. Others were biennials or short-lived perennials which were able to adjust themselves to a short period of favorable conditions.

SHRUB THICKETS

Areas dominated by postclimax shrubs were limited in extent and occurred only in the most mesic habitats. Most of the shrubs grew on north- and east-facing banks of ravines, in narrow ravines, and in other local, protected places (Fig. 21). One typical shrub community, for example, was located on a steep northeast slope. It extended from the middle of the slope to the middle of the comparatively narrow ravine. Switchgrass, wild rye, and Indian grass, as well as the more common big bluestem, were intermixed with the shrubs near the margin of the thicket. The first two species were usually more abundant near the shrubs or intermixed with them than anywhere else in the prairie. A dense stand of *Toxicodendron rydbergie*, which completely encircled the thicket, extended out into the tall grass as well as several feet under the shrubs. The next zone consisted of *Prunus melanocarpa* Shafer, *Ribes odoratum*, and *Grossularia missouriensis*. These shrubs were 3 to 5 feet tall, and in places they were almost completely covered with *Vitis vulpina*. *Prunus americana*, which was about 12 feet tall, occupied the most mesic part of the habitat at the base of the slope.

FIG. 21. Shrub thicket in a pocket on a northeast slope.

A small *Ulmus americana* was located at each end of the thicket. Where the shrubs were more or less open, tall grasses and certain mesic forbs were intermixed. These included *Solidago altissima, Helianthus divaricatus, Vernonia baldwini, Monarda mollis*, and *Asclepias syriaca*.

On west or south exposures, shrubs were either entirely absent or grew thinly mixed with tall grasses. The Rosa, Amorpha, and Symphoricarpos were most common in these places, as partial protection resulted in the dwarfing or total elimination of others which required most moisture.

In the well-watered, deeper ravines, where considerable protection was furnished, *Populus sargentii, Fraxinus pennsylvanica, Acer negundo*, and *Ulmus americana* grew to heights of 50 or more feet. Here shrubs were present as an understory in an almost impenetrable thicket. These shrub communities are of much value to wildlife as they furnish both food and cover for game and songbirds.

ECOTONES

Transition zones between plant communities were quite variable and, like the distribution of the communities themselves, they depended considerably on the slope and exposure. Another modifying feature was the presence and nature of catsteps. Vertical distances between catsteps ranged from a few inches to 2 or more feet. Horizontal distances between them

were only 1 to 2 feet on steep slopes but several yards on gradual ones. Abrupt changes in the types of vegetation were often associated with catsteps. Where there were none, ecotones were quite broad.

The change from the short-grass type to mixed-grass vegetation was usually over a rather broad ecotone with the mid and tall grasses gradually becoming more abundant toward the base of the slope. However, when a catstep was present on the upper portion of a hillside, the short grasses were abruptly replaced by mid and tall grasses, and the mixed-grass type was mostly absent. Usually the mixed-grass type, but often the short grasses, extended to the upper edge of the catsteps. Then either one or the other of these occurred below the zone of mid and tall grasses. An abrupt and distinct change in slope also usually resulted in a very narrow ecotone.

The ecotones about the wheat grass type were also usually narrow. Adjoining communities under normal conditions were never able to invade the territory of established wheat grass. Wheat grass, however, often extended its area considerably by means of rhizomes several feet in length. Thus, it became a part of many contiguous communities, if indeed it did not replace them.

Where the tall grasses adjoined a shrub thicket, there was ordinarily a narrow transition zone where they intermingled. This was sometimes only 3 to 4 feet wide, but if the shrubs were dwarfed, grasses extended completely through the thicket.

Some of the variations that occurred on different types of hillsides are shown in Figure 22. Transect A sloped gradually to the east until a catstep was reached when the slope became greater. The upper edge of the catstep was covered with mid grasses over an area little more than a foot wide. Short grasses were not present below the catstep. Transect B illustrates a north-facing slope where there was a series of small catsteps on a gradual slope. Had the catsteps not been present, this hillside would have been covered entirely by the mixed-grass type. Here the mid- and tall-grass type was present on the catsteps, which caused the mixed-grass type to be divided into two zones. Transect C illustrates the mixed-grass community being divided into two portions by an alterne of short grasses. This change in vegetation was probably due to the change in degree of slope.

PLANT PRODUCTION

Dry weight of plants is one of the best quantitative characteristics of vegetation (Hanson 1938), and increase in dry weight is the best measure of growth (West, Briggs, & Kidd 1920). The vegetation in each community was removed by means of a hand-clipper. Unlike a mowing machine, this clipper removed the short grasses to the same general level as the taller and more easily harvested mid and tall grasses. Actually the mower used in cutting the grass for hay leaves at least 40 percent of the short grass standing as stubble. The plants were clipped at the end of each growing season in 100, square-meter quadrats at a height of about one-half inch above the soil surface. The short grasses, mid and tall grasses, and forbs were clipped, air-dried, and weighed separately in order that their yields could be compared.

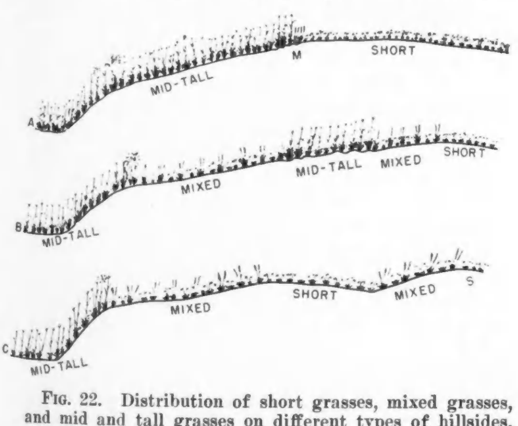

FIG. 22. Distribution of short grasses, mixed grasses, and mid and tall grasses on different types of hillsides. (M) in the upper transect refers to a very narrow zone of mixed grasses.

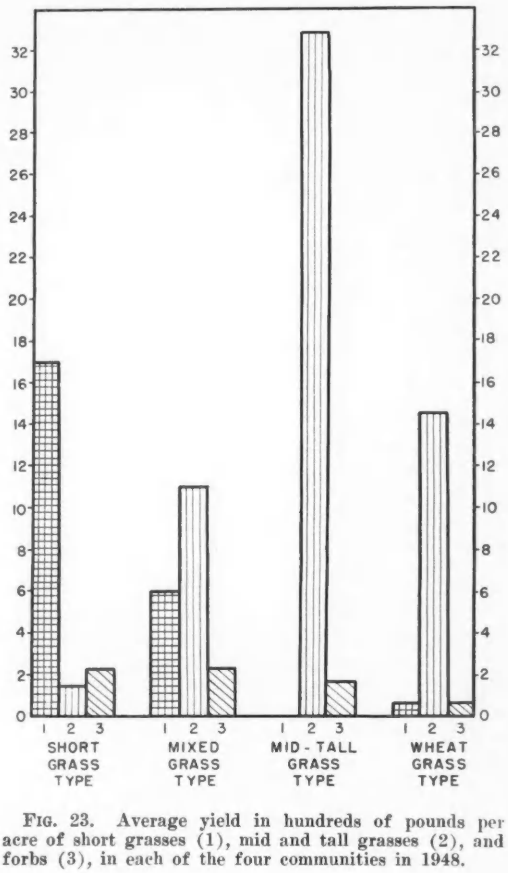

FIG. 23. Average yield in hundreds of pounds per acre of short grasses (1), mid and tall grasses (2), and forbs (3), in each of the four communities in 1948.

The amount of plant material produced in each of the communities in 1948 is shown in Figure 23. Total yields were greatest in the mid- and tall-grass type where the amount of vegetation produced was more than 3,400 pounds air-dry forage per acre. The maximum yields in certain "hay pockets" in the most mesic portions of the lowlands were as high as 2.5 to 3.5 tons per acre. There was little difference in production in the short-grass and mixed-grass types: both yielded about 1 ton per acre.

As regards partial yields, short grass furnished 77 percent of the vegetation in its type and 29 percent in the mixed-grass community. Where the latter type consisted of wheat grass and short grass, the short grass produced about 50 percent of the total yield. In the wheat grass type, more than 95 percent of the total yield was wheat grass. Over the entire prairie, forbs furnished only 7 to 8 percent of the total yield.

DEGENERATION OF PRAIRIE

The first stage of degeneration of prairie occurs when grazing is practiced under a system of good range management. There is only slight change in the composition of the vegetation, since moderate grazing is not harmful to the prairie as a whole. Further degeneration is caused by overgrazing and poor range management, which result in drastic changes in vegetation. The plants are weakened, the cover is thinned, and erosion becomes common and often severe. Following the plan of Weaver and Hansen (1941), stages in degeneration have been classified according to the resulting grades of pasture into four more or less distinct groups. According to the composition of the vegetation, its condition, and the forage yield, these are designated as excellent, good, fair, and poor. All grades have originated from prairie (Branson 1951).

In climax prairie undisturbed by grazing, local disturbances resulting in subseres occur chiefly as a result of digging by badgers, construction of mounds by pocket gophers, stacking of hay, and man-made trails. In some prairies subseres are caused by drought or by deposition of wind-blown or water-carried soil. These areas may vary from a few square feet to many acres in extent. Small tracts of native vegetation of 10 to 20 acres were found in parts of fields where the land was inaccessible or too rough for cultivation. Soil deposition from adjacent cultivated fields was common and resulted in the partial replacement of native vegetation by weedy grasses and forbs. Many lowlands, even in some of the larger prairies, were atypical due to deposition of soil carried down ravines from higher cultivated land or abandoned fields or even from adjacent overgrazed pastures.

DISCUSSION

Since no ecological study had been made on the vegetation of the central loess hills preceding that of Weaver and Bruner in 1945, the predrought condition of the vegetation will never be known. However, the changes wrought by drought in the prairies both south and east of the area are fully recorded and the course of succession has been followed in detail. Therefore much may be inferred as to what occurred in the loess hills, both as regards amount of destruction and stages in recovery. It is certain that the changes in composition and distribution of the communities were very great and that the original condition has not yet been re-established.

Albertson (1937) has shown that at Hays, Kansas, about 150 miles southward, approximately 23 inches of precipitation supports a basal area in the short-grass type of 70 to 90 percent. It would seem that a similar precipitation in the loess hills should support a larger basal area than 31 percent. In fact, this does occur where buffalo grass is present. It has been shown that the predrought cover of about equal amounts of buffalo grass and blue grama southward and westward was replaced after drought by one with two-thirds buffalo grass and one-third blue grama (Weaver & Albertson 1944). In the loess hills buffalo grass is not abundant and blue grama has been slow to reclaim areas lost during the drought. In addition to its slow vegetative spreading, seedlings have probably been suppressed by hairy chess which grew in extremely thick stands and only recently has become less plentiful. Buffalo grass is more susceptible to drought than blue grama and was undoubtedly killed back to some extent. However, since it recovers rapidly, it has possibly never been more abundant than it is now. The type of soil preferred by buffalo grass, as illustrated by its occurrence in trails and on other compacted soils, is present only locally. The relatively coarse, unstable, loessial soils are, like the sandhills westward, more favorable to bunch grasses than to sod formers.

The mixed-grass type extended completely over the top of some of the lower hills and joined the mid- and tall-grass type near the lower slopes. This condition was probably more prevalent before the drought and caused the short grasses as a type to be restricted to the highest and driest hilltops. Mid grasses were completely destroyed in less favorable parts of their habitat. Their restoration will be slow since sand dropseed was the only mid grass with ample viable seed on the ground after the drought to restore its cover (Weaver & Mueller 1942). The wheat grass-blue grama community, which is only a variation of the mixed-grass type, has increased rapidly since the drought. This has been due mostly to the invasion of wheat grass into thinned stands of short grass.

The wheat grass type, where other species are largely excluded, probably occurred before the drought only in very limited localities which had been disturbed by other causes than drought. From these places, and from plants more generally distributed throughout the prairies, wheat grass has spread rapidly following the death of the other grasses. It is by far the most rapidly spreading of the few cool-

season grasses present and was able to increase its area during the cool, moist weather of spring. Thus, except in the years when spring rainfall was light as in 1948, wheat grass had the advantage over the warm-season grasses which renew growth later and are more dependent on summer rainfall. Having become established, wheat grass will probably be replaced by other grasses only after a series of years when the weather is unusually favorable to warm-season grasses. The presence of this invader has decreased the value of the prairie by its detrimental effects on the soil, by poor quality of its hay, and by suppression of more desirable species. Where grazing is practiced, this species is valuable in that it furnishes forage early in the spring when it is palatable.

One of the outstanding features of the vegetation is the great extent of roots. The subsoil, with a high silt content, is permeable and moist and offers an excellent medium for root growth. Despite great length, more than 90 percent of the root weight occurred in the A horizon (Weaver & Darland 1949).

SUMMARY

The native vegetation of the loess hills in Custer, Buffalo, Sherman, and Valley counties in central Nebraska belongs to the mixed prairie association and is an important agricultural resource of the state.

Thick mantles of loess were deposited on this area during Tertiary and Pleistocene times. Headwater erosion has formed the characteristic canyon topography of the region. Water penetrates rapidly through Peorian loess, but at the contact with the Loveland, its penetration is retarded. Hence, the ground water is directed laterally causing the overlying Peorian loess to slip valleyward. Catsteps are thus formed.

Well-developed upland soils are of the Holdrege series, while the lighter-colored immature soils belong to the Colby series. Concentrations of carbonates are mostly confined to depths between 3 and 6 feet. Silt content of all samples was usually between 50 and 60 percent, and there was often less than 15 percent sand. Hygroscopic coefficient to a depth of 8 feet was usually from 8 to 10 percent. Organic matter ranged from 3.5 to 5.1 percent and nitrogen from 0.183 to 0.283 in the surface 4 inches of soil.

Of the four communities of grassland, the short-grass type or faciation occupied approximately 33 percent of the area. It occurred on most of the hilltops and xeric slopes. The mixed-grass type of short and taller grasses, which also covered about one-third of the area, was typically located on the hillsides and occasionally extended over the hilltops. The mid- and tall-grass type (postclimax associes) furnished about 25 percent of the grassland. It was best developed in broad, flat lowlands but also occurred on steep banks of the ravines, on catsteps, and other protected places. The western wheat grass type, dominated by *Agropyron smithii* alone, is a product of the drought and has appeared wherever the normal vegetation has died or where its cover has become open enough to allow invasion. Once established it is a strong competitor. By early use of all available water and adverse effect on soil structure, it eliminates nearly all other species.

The station in *Agropyron smithii*, located at the base of a slope facing southwest, had the highest air and soil temperatures and the lowest relative humidity. Differences in soil temperatures between types were considerably less at a depth of 6 inches than at the surface. The mid- and tall-grass type and shrub thicket in the lowland were the most mesic. Average daily water loss from atmometers was 6.5 cubic centimeters in the mid- and tall-grass type as compared with 23.8 cubic centimeters in the short-grass type. Average daily wind movement was .77 and 4.23 miles per hour at the same stations, respectively.

Precipitation in April and May of 1948 was 4.85 inches below normal. That in June and July was 4.68 inches above normal. Distribution was more nearly normal in 1949, but total amount was somewhat less.

Available soil moisture during the first year in the short-grass type, except in the surface foot, was usually less than 5 percent to a depth of 4 feet. More moisture was present early in the season in 1949; until the third week of June, more than 10 percent was available to a depth of 3 feet. Between depths of 4 and 8 feet, 5 to 8 percent was available for growth throughout both seasons.

Considerable runoff on the hillsides resulted in less infiltration of current precipitation. This runoff from uplands resulted in increased moisture in lowlands, where more than 10 percent was often available in the upper 3 feet of soil. The deeply rooted grasses caused a gradual decrease in soil moisture below 4 feet throughout both seasons, since current moisture never penetrated beyond this depth.

Less moisture was present in the soil where *Agropyron smithii* was the dominant than in any other community. The catsteps furnished a marked contrast in that they had more than 10 percent available moisture present at almost all times.

In the short-grass type, *Bouteloua gracilis* comprised 90.9 percent of the vegetation and was present in every quadrat studied. It is the most drought resistant of all the native grasses: when the soil is dry it becomes dormant but resumes growth when moisture becomes available. The roots extended to a depth of about 6.5 feet. *Buchloe dactyloides* increased the basal area greatly where present, but it was seldom an important species. *Carex pennsylvanica* and *Carex eleocharis* occurred in 80 percent of the quadrats but composed only 1.1 percent of the total basal area. *Agropyron smithii* was the only mid grass of importance in this type. Average basal area was about 31 percent. It was quite uniform and was seldom less than 20 percent or more than 40 percent. There was an average of 1,743 pounds per acre of air-dry mulch on the surface of the soil.

In the mixed-grass type, *Bouteloua gracilis* was also the most important component. It furnished 49.5 percent of the vegetation, sometimes as small patches alternating with mid and tall grasses but more frequently as an understory to the taller grasses. *Bouteloua curtipendula* was the most important mid grass; it composed 17.7 percent of the basal area and was present in 83 percent of the quadrats. Roots extended below a depth of 8 feet. *Sporobolus cryptandrus* was present in 64 percent of the quadrats. It seemed most abundant where considerable disturbance by drought was evident. *Agropyron smithii* was an important species which often shared dominance with *Bouteloua gracilis* alone. *Koeleria cristata* and *Panicum wilcoxianum* were widespread but furnished only a small part of the basal area. Both have shallow root systems. Sedges were present in 97 percent of the quadrats and composed 6.8 percent of the vegetation. *Andropogon furcatus* was the only tall grass commonly present in this community. Average basal area was approximately 19 percent, and there was an average of 993 pounds per acre of mulch.

The mid- and tall-grass type had the largest number of species. *Andropogon furcatus*, the most abundant, furnished 56 percent of the vegetation and occurred in 90 percent of the samples; it often occurred in nearly pure stands. In the most mesic sites, *Sorghastrum nutans*, *Elymus canadensis*, and *Panicum virgatum* were intermixed with *Andropogon furcatus*.

Bouteloua curtipendula ranked second in importance; it was sometimes intermixed with *Andropogon furcatus* but more often with *Agropyron smithii*. *Poa pratensis* formed an understory on lowland. It grew rapidly when light was plentiful early in the spring and again in the fall after the tall grasses were mowed. Various sedges were widely distributed. Basal area varied from 2 to 15 percent and the average was 9. Where the grass was never mowed, there was an accumulation of about 15,000 pounds per acre of mulch, but where mowed annually, an average of only 838 pounds accumulated.

Forbs contributed but little to basal area but their dense growth in societies sometimes caused a reduction in yield of grasses. The most abundant were *Lygodesmia juncea, Amorpha canescens, Erigeron ramosus, Ratibida columnaris, Psoralea tenuiflora, Aster multiflorus, Gaura coccinea, Toxicodendron rydbergii, Rosa pratincola*, and *Solidago glaberrima*. The most valuable forb was *Amorpha canescens*, which was widely distributed and highly palatable.

Layering was evident both above and below the soil surface. Tall, mid, and short grasses were 4 to 6 feet, 2 to 3 feet, and 5 to 12 inches tall, respectively. Although roots of some grasses were confined to the upper 3 feet of soil, those of the most important ones and some of the forbs extended 6 to 10 feet in depth. Other forbs were much deeper.

Each of four seasonal aspects was characterized by the flowers of certain forbs and grasses.

The most mesic sites in ravines and their steep protected banks were occupied by small trees, shrubs, and certain forbs.

Ecotones varied from a few inches to several yards in width depending on the slope, exposure, and presence of catsteps.

Greatest yields were obtained in the mid- and tall-grass type, which produced over 3,400 pounds of air-dry forage per acre in 1948. The short-grass and mixed-grass types each yielded about a ton per acre.

The prairie degenerates following grazing. Subseres are also caused by local disturbance or by drought. Both composition and structure of the vegetation were greatly modified by the drought of 1933-40. The prairie is not yet restored to its normal condition.

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FLUCTUATION OF NON-FOREST ANIMAL POPULATIONS IN THE UPPER MISSISSIPPI BASIN

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I. INTRODUCTION

The interpretation of the causes of variation in the size of populations of organisms has usually been found difficult. Correlations with weather conditions has been most frequently attempted and usually with only partial success. It is the purpose of this paper to present a large body of evidence to the effect that ultraviolet light is a reproductive stimulus and constitutes a factor paired with moisture which initiates the control of the size of populations. Relative to ultraviolet light Sabrosky, Larsen, and Nabours (1933) have shown that violet and ultraviolet light are a reproductive stimulus evidently imparting vigor to the young in a grouse locust. Likewise, Marshall and Bowden (1934) showed that ultraviolet light speeded up oestrous in the ferret to a marked degree and that the results were brought about through the functioning of the eye.

In the cases analyzed it appears that moisture, probably largely in the form of vapor pressure, is paired with solar ultraviolet light as a reproductive stimulus much as temperature and humidity are paired to give us a sense of comfort in a series of combinations of the two (Lamb 1910). It has been demonstrated in some cases that rainfall influences survival and mortality especially among the young stages. Evidence will be also presented to the effect that ultraviolet light is a potent factor and acts as a stimulus in only a narrow band of intensity. Intensities above and below the narrow band of optimum are associated with smaller populations, indicating detrimental effects on the individuals.

It is a further purpose to present evidence that physical factors effectively influence reproductive vigor only during a short period. In the case of some species the period for ultraviolet light comes in the life of the adult, and in the case of other species and factors, the effective period is concerned with the success of the young. Both are often periods of effective influence on population. Data will be presented to show that in some cases the limits of favorable and unfavorable weather may be determined by an analysis of published Weather Bureau data considered in relation to population size. It will further be shown that there is no direct relation between sunspots and the size of populations; that the indirect relations are characterized by some of the same unpredictable irregularities that characterize weather phenomena. To present these data it was necessary to examine the record not only of chinch bug population hibernating in a sixty-acre woodland, but also to carry the analysis back to the beginning of the record in 1823. Similarly it was necessary to utilize quail data for several localities, in one case back to 1925, and rabbit data for the states of Illinois and Wisconsin.

The original observations and quantitative collections utilized in the paper were made in the William Trelease Woods. The study was begun in 1933 to provide data freer from error than that provided by pest control and commercial operations. The results of the study of strictly forest species will be reported in another paper (Shelford 1951).

The woods is located at Latitude 40° 8′ North and

Longitude 88° 9′ West, six miles E.N.E. of the University of Illinois campus at Urbana, Champaign Co., Illinois. It is a tract including nearly 50 acres of nearly virgin deciduous forest with American elm (*Ulmus americana*, L. 18%) and sugar maple (*Acer saccharum* Marsh, 28%) making up 46% of the stand (Vestal & Heermans 1945). The region was originally characterized by a tall grass prairie interspersed with deciduous forest groves and stream-skirting forest. The natural forest-edge or margin grades from forest trees to small trees such as hawthorns and wild plum, to shrubs such as witch hazel and to rank forbs next to the prairie grasses.

This edge vegetation provides shelter and nesting places for the vertebrates noted above and some invertebrates. The vegetation of the woods proper serves as shelter for the non-forest animals only during the fall and winter and early spring months. The presence of these species during the colder portion of the year and absence in the warmer portion indicates a rather distinct migration by the invertebrates from the field and grass-covered areas into the woods in the autumn and out again in the spring. The vertebrates merely enter the woods much more frequently in winter. Since the vegetation and accumulated litter of the woods serve only as shelter for invertebrates, the character of the vegetation is unimportant.

The writer is indebted to the persons named below for assistance in extending the curve for chinch bugs on 120,000 square miles from 1940 through 1947 and for help in related problems: L. Haseman, University of Missouri; Claude Wakeland, U. S. D. A. Agricultural Research Administration; George C. Decker and J. H. Bigger, Illinois State Natural History Survey; Paul O. Ritcher, University of Kentucky; E. L. Chambers, University of Wisconsin; and H. M. Harris, Iowa State College. For data on pasture conditions in Illinois, thanks goes to J. A. Ewing of the Illinois Crop Reporting Service at Springfield and for assistance with the manuscript to Mr. Ross J. Miller of the Department of Zoology, University of Illinois. Permission to use the Natural History Survey's data on cottontail rabbit populations, granted through R. E. Yeatter, was of great value. The writer is indebted to Dr. S. C. Kendeigh for assistance with the manuscript. Special acknowledgment is due the Research Board of the Universtiy of Illinois and to Deans R. D. Carmichaeal and L. N. Ridenour for continuous financial support 1934 through 1950.

1. Physical Conditions of the Area

The elevation of the Trelease Woods above sea level is approximately 700 ft. The mean annual rainfall is 36.5 in. (92.7 cm.) with the greatest amount in summer. The May average is highest (3.83 in. or 9.7 cm.) and June, second highest (3.74 in. or 9.4 cm.). The mean annual temperature is 51.2° F. (10.67° C.). The discussion of the long-time chinch bug records for an area of 120,000 sq. mi. (310,800 km^2) considered by Shelford & Flint (1943) will be reconsidered, but the average meteorological conditions of this area as a whole are well represented by the figures given for Urbana, Illinois, which is near the center of this large area which includes small portions of the surrounding states of Wisconsin, Indiana, Kentucky, Missouri, and Iowa. Since 1860 the rainfall has varied from 25 in. to 50 in. in extreme years. The detailed records of the Weather Bureau have been used (see Hartzell 1916).

Solar phenomena influence weather and organisms, both directly and indirectly. Other phenomena such as electrical conditions and the amount of ultraviolet or other types of radiation are understood to have important biological effects. The character of solar phenomena has been made clear only in recent years. Stetson (1947) states that Bethe worked out a "true explanation of the source of solar energy." "Explosions do occur on the sun" which may be compared to an atomic bomb explosion.

According to recent works on the sun (Stetson 1947, Menzel 1949), that portion of the sun lying outside the zone of complete opacity is called the solar atmosphere. The outer boundary of the sun which produces a continuous spectrum is called the chromosphere. The corona is a halo which is visible at the time of a total solar eclipse. Sunspots are commonly referred to as solar cyclones. At the same time they are powerful magnets which cause magnetic disturbances on the earth. Variations in the magnetic fields of sunspots may be extremely important "because . . . such variations may produce electric currents that will heat the chromosphere and corona. And a bright chromosphere or coronal region will send out ultraviolet light or even x-rays with high ionizing power. Ordinary prominences seem to cause no marked terrestrial disturbances." "Bright aurorae and ionospheric disturbances all increase with sunspot numbers." The correlation with spots is not striking because "sunspots as such are not fundamental" (Menzel 1949, pp. 305); sunspot numbers are not an accurate index of solar activity (p. 114).

However, solar flares, which are brilliant prominences, appear to differ from the ordinary prominences. Baker (1946) states that solar flares are accompanied by outbursts of ultraviolet radiation. This is said to last from one-half hour to two or three hours. It is further suggested that the earth is bombarded with ions from the sun. There are electrified layers in the earth's atmosphere at a height of 70 to 250 miles, called the ionosphere. "The electrification is largely due to ultraviolet energy from the sun which tears electrons away from atoms and molecules in the upper air" (Menzel 1949, p. 297).

From 1924 through 1938, Pettit (1932) at the Mount Wilson Observatory, measured ultraviolet light with very complicated equipment (International Astronomical Union, 1924-38). Pettit expressed the ultraviolet intensity as the ratio of the energy of wave-length 320 mμ to that of 500 mμ in the green.

The ratios may be 0.94, 1.35, etc., and are used as indices in this paper without the decimal point.

Menzel (1949, p. 312) states that the amount of ozone varies with the sunspot cycle and the amount of ultraviolet reaching the earth undergoes change as a result. Stetson (1947, p. 33) expresses what biologists would call the regulatory effect of ozone on ultraviolet as follows: "The amount of ultraviolet light from the sun used up in making ozone will never reach the earth's surface at all. Moreover, the thicker the ozone layer, the more ultraviolet radiation is absorbed in it. So you see that during 1928, when the sunspots were most numerous, the intensity of the ultraviolet rays from the sun may have been so great as to create a very thick layer of ozone in the upper atmosphere, which in turn would cut off from the earth's surface a great deal of this ultraviolet radiation that was actually responsible for the increased ozone. This may be the explanation as to why there was a drop in the amount of ultraviolet radiation measured by Dr. Pettit's apparatus just at the time of sunspot maximum, when we might have expected the greatest amount to be recorded.

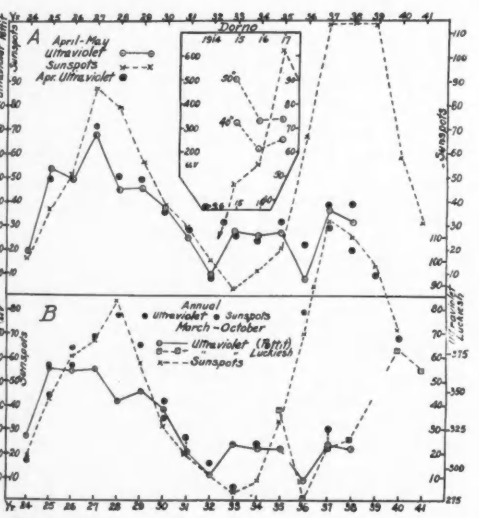

FIG. 1. Sunspot-ultraviolet relations. All scales except Luckiesh's are essentially arbitrary.

The upper section, A, shows the April-May ultraviolet and April-May sunspot relative numbers as line graphs and the April ultraviolet by solid circles whenever it differed from the April-May value. The insert represents the 1915 to 1917 averages of ultraviolet of Dorno's readings. Those marked 50° are for August alone. Those marked 40° cover August and September.

Lower section, B, shows the mean March through October ultraviolet (Pettit's (I.A.U.) indices, decimal point omitted) and the relative sunspot numbers (I.A.U., Zurich). The encircled x's show the mean sunspot average for the entire year when it differed from the March-October value. The black circles show the mean ultraviolet for the year whenever it differed from the March-October value. The Luckiesh data are shown for 1935-1938 and two proportional estimates for 1940 and 1941 in mean monthly E-vitons per cm.² For comparison of these with other records see p. 164.

"When the sunspots subside, it seems quite likely that the sun sends us less ultraviolet light so that the rate of production of ozone in the upper atmosphere of the earth will, in general, follow a decline in the sunspot curve. If the ozone layer, however, thins very much, it will be less efficient in screening the ultraviolet rays from the surface of the earth. So, we momentarily find in Dr. Pettit's measures that there will be times when the ultraviolet light seems to grow stronger at sunspot minimum, for ozone rapidly decomposes unless the supply of ultraviolet rays from the sun is kept up." The March through October mean of monthly average of sunspots and of Pettit's ratio of ultraviolet light (1924-1938) as shown in the lower half of Fig. 1 is a graphic representation of the facts quoted from Stetson.

The period 1915 to 1918 is illuminated by Dorno (1919), who measured ultraviolet light with a cadmium phototube in Davos (Switzerland) Lat. 46° 50′ N. His readings were as follows:

Sun's Elev. 40°	Aug.-Sept.	1915, 325;	1916, 230;	1917, 254.
Sun's Elev. 40°	Apr.-Sept.	....	1916, 229;	1917, 216.
Sun's Elev. 50°	Apr.-Aug.	....	1916, 326;	1917, 304
Sun's Elev. 50°	Aug.	1915, 505;	1916, 330;	1917, 338.
Sun's Elev. 40° & 50°	Oct.	40°, 1917, 208;		50°, 1918, 125.

There was a sharp increase in sunspots in 1915, 1916, and 1917 (maximum). Dorno's readings show that the ultraviolet declined sharply between 1915 and 1916, the years of sharp sunspot increases, and remained at the 1916 level in 1917 in accord with the relationship brought out by Stetson (1947). (See also Huntington 1941.)

Luckiesh, Taylor & Kerr (1937, 1939, 1944) made sun and sky measurements of ultraviolet light with a cadmium-magnesium alloy phototube sensitive to wave lengths shorter than approximately 335 mμ. maximum sensitivity at 280 mμ at Cleveland, Ohio. Latitude 41° 30′ N. They expressed the readings in terms of minimum perceptible erythema as MPE hours. Their physical measure, the E-viton, is the equivalent of 100 ergs cm² or 10 microwatts sec/cm² or two thirds of an MPE hour (E-viton 40 min/cm²). One E-viton acting for 40 minutes or ten E-vitons operating for 4 minutes, will redden untanned skin. The figures presented (Luckiesh 1946) are the summations of units in terms of hours from day to day and month to month. For the years 1935-38 he presents monthly figures in a graph. For 1940 and 1941 only the totals are available (Luckiesh 1946) and unfortunately the records were not preserved for 1939 and the months of 1940 and 1941. High 1940 and 1941 sums follow Stetson's general rules.

Pettit (1932) made his published readings on clear days but also showed by the use of phototubes, etc., that 25% of the ultraviolet which he measured came through the clouds on overcast days and much more when moving clouds nearly covered the sky. His minimum reading was 10% during a rainstorm.

In using the Pettit data, no cloudiness corrections were made. Ratios based on the intensity of a relatively stable (500 mμ) and of a variable (320 mμ) wave length through the upper atmosphere near midday are indicators of astronomical ultraviolet intensity. Readings through the lower atmosphere reflect the length of the atmospheric path, transparency of the atmosphere, etc. There are three (one each in April, June, and Sept.) essentially coincident readings of Pettit and Luckiesh, et al. (1937) which show that the midday readings of Pettit may remain nearly the same while the readings at Cleveland vary greatly due to seasonal changes in the length of the atmospheric path (Luckiesh, 1946, p. 50).

Coblentz and Stair (1936, 1943) published midday readings of ultraviolet covering 1934 through 1942 which were represented by dots plotted on air mass figures and microwatt sec/cm^2. A few dots were dated. It did not seem practicable to make use of these values because of the large variations in such readings from day to day and the rather long exposures required by animals. The same authors (1944) published summations for two years and erythermal data in ergs. This work was summarized and extended by Coblentz (1945). The measurements which he reported covered the ultraviolet of sun and sky in Washington, D. C., Lat. 38° 55′ N., 1941 through 1945, with a Zr phototube. He presented his results in ergs and milliwatt min/cm^2 at 313.2 mμ and shorter. His summations as read from his figure (1945, p. 116) are as follows:

	1941	1942	1943	1944
Annual Sum	7115	6815	7650	7030
Apr.-May Sum	1850	1540	1890	1540
April Sum	800	640	770	550

Large values for May, June, July, 1943, are attributed to unusually clear skies. The Cleveland 3147 sum of E-viton hours for 1941 must be divided by 2.5 to reduce it to milliwatt min/cm^2, which gives a value of 1259 for Cleveland, while the Washington figure is 7115 as read from Coblentz's (1945) chart. The Luckiesh data are roughly 17.6% of Coblentz's readings. The same ratio holds for their respective values for minimum perceptible erythema. This difference probably results from the differences in the wave lengths measured and from "being erythemally weighted" (Luckiesh 1946, p. 103). The Cleveland figures have merely been arbitrarily raised to the Washington level, on the basis of the 1941 overlapping readings, for plotting and year to year comparisons. However, no use is made of the figures except for the chinch bug and none of the winter readings of Kendrick & Oritz (1938) or Kendrick & Del Toro (1940) in Puerto Rico were utilized except for general comparison of 1938 and 1949. Kendrick & Del Toro show the ultraviolet intensity to be higher in 1939 than 1938.

Sunspot numbers for April and May have been used against the background of ultraviolet data in interpreting the earlier chinch bug history. It is not clear, however, that this use of two month averages offers any advantage. Pettit (1932) used the three-month average daily number of sunspot groups and the solar ultraviolet ratio treated in the same way, in comparing the two. According to Baker (1946) the number of groups, available only since 1897, is a better index of solar activity than the number of spots (Nicholson & Moulders 1942). Since sunspots are not an accurate indication of solar activity the results of direct correlations will always be uncertain.

In addition to sunspot numbers, the International Astronomical Union (Zurich) published the character figures for four types of flocculi (bright patches on the sun). Garcia-Mata & Shaffer (1934) made use of faculae (flocculi). (See Dewey, E. R. & E. F. Dakin 1947). An examination of these records in relation to the critical spring months, led to the unavoidable conclusion that correlations of Pettit's ultraviolet readings are best with sunspots.

II. PRINCIPLES GOVERNING THE USE OF WEATHER AND SOLAR DATA TO EXPLAIN POPULATION CHANGES

The analysis of weather and solar data for the purpose of finding correlations between physical conditions and population size is laborious and time-consuming. It is important, therefore, to point out the methods that have led to the successful finding of well supported correlations.

The general vigor and reproductive capacity of most organisms vary from time to time. The term reproductive potential may be used to cover the entire physiological condition of an animal and its offspring, beginning with the general vigor of the parent, the vigor of the eggs, the number of eggs produced, and the vigor of the young expressed in their ability to grow to normal maturity. Assuming the reproductive capacity to be at its ideal maximum, other forces operate to check the growth of the large population which will naturally result. The external physical conditions may weaken and destroy the eggs and the young stages or even the adults. Chapman (1928) has called the reproductive capacity or potential, in the sense outlined above, biotic potential. (In ecology biotic is ordinarily applied to the aggregation of plants and animals on an area.) Chapman designated biotic potential by the symbol Bp. He summed all the factors in the environment which tend to reduce populations, designating this by R. Population, which he called concentration of individuals, he designated by C. Thus he wrote his formula $C = Bp/R$. He made some progress in substantiating this formula in a study of populations of the flour beetle (*Tribolium confusum*) . It appears to be a rather too formal statement of a highly complicated problem of natural populations. He appears to assume that the high reproductive potential is always present. Or at least he did not take into consideration such enormous variation of this property as was demonstrated for the chinch bug by Shelford & Flint (1943).

The several relationships suggested by Chapman's

formula and the related discussion must be analyzed. This analysis can be accomplished in some cases by careful study of collected samples.

(1) The first step is, insofar as possible, to separate change in abundance due to fecundity from that due to mortality.

(2) The general life history pattern must be determined. (a) Are there one or two or more generations, broods, or litters in a year or season? (b) Does the species pass the winter in the adult, egg, or an early developmental stage? (c) If the winter is passed in the adult stage, at what time in the following spring do the old generation individuals reach sexual maturity, mate, and disappear; when do the new ones take their places? (d) If there are two broods of adults, when are the older ones replaced by the younger ones? (e) Are there additional broods, litters or generations in long favorable open seasons?

(3) The determination of the sensitive periods in the life history or in the annual cycle of physiological conditions in organisms living more than one year is of the utmost importance.

1. Location of Sensitive Periods in Life Cycles

Johnson (1924), using the records of the condition of sheep and of the lamb crop as reported in the Live Stock Journal, London, found that when the production and growth of lambs was high and the condition of the industry excellent, the months in which the lambs were born fell within very narrow limits over a period of many favorable years. He worked mainly with temperature and humidity. In dealing with wild species the method is a simple one. The two sets of weather conditions are laid out on the ordinate and abcissa of a coordinate paper. The points representing the condition of the two factors being tested are plotted for the years in which there were large increases of population of a species. Then, if some one month shows a very limited range of variation in respect to the two factors, while other months show great variation, it is assumed that the month in which conditions are nearly the same from favorable year to favorable year represents a critical period for the individual of the population. This was borne out by the sheep records but the conditions affected survival more than fecundity (see Fig. 6, p. 158). However, taken alone, such diagrams do not necessarily show whether mortality or fecundity is involved. Gregory (1948) has summarized the knowledge of sensitive periods in plants.

Shelford (1927, p. 353) showed the limits of months associated with large codling moth populations. In this case large populations were associated with high October rainfall and the breaking of dormancy, more rapid development and better reproductive potential. This least variation method may be applied to a number of combinations of factors with illuminating results. The amount of time and labor involved in many of these operations is almost prohibitive. Ultimately, the results of these correlations and combinations are a guide in experimental work. One must change from observations in nature to experiments in the laboratory in making interpretious population changes.

2. The Use of Thermohygrograms, Etc.

A type of diagram frequently referred to as the thermohygrogram is concerned with two factors which operate together usually physiologically. Probably the oldest and best known example is the combination of temperature and humidity which gave a sense of personal comfort (Lamb 1910). One is comfortable when at rest at 78° F. and 20% humidity, 74° F. and 40% humidity, or 65° F. and 80% humidity.

Pierce (1916) using temperature and humidity on the cotton boll weevil, showed that the equal survival lines had the form of parallel ellipses (see Figs. 14 to 19, p. 171). Huntington (1919) examined many thousands of human deaths in relation to temperature and relative humidity in percentage of saturation as recorded by the Weather Bureau. By combining his records for southeastern United States, southern France, and northern Italy, much of the climatically possible combinations of daily temperature and humidity was covered and a composite chart was drawn by Shelford (1929a, p. 269). In this diagram the equal survival lines form a series of concentric half ellipses.

A study of the rate of development of the stages of the codling moth, a pest of the apple, Shelford (1927) utilized a series of experimental chambers. Thermohygrograms showing equal rates of development were established by checking against a large series of out-of-door records for the pre-pupal stage of the larva, the egg, and the pupal stage. The equal rate lines form portions of ellipses.

The following is a list of additional thermohygrograms which have come to the attention of the writer: (1) Bodenheimer (1928, 1930), percent of mortality of the eggs of the desert locust; (2) Zwolfer (1933), several stages of *Lymantria monacha*; (3) Larsen (1943), the mortality of the common house fly. In addition, Hall (1925) found a similar relationship beween the development of the white fish embryos and the hydrogen-ion concentration and oxygen content of the water, and Willmer (1933) shows one for respiration of a tropical fish for CO_2 content with O_2 content, and one for CO_2 content with pH of the water. Shelford (1932, Figs. 3-10, pages 507-514) developed thermohygrograms for each of the several life history stages of the chinch bug. Nearly all the charts are concerned with rate of development or with time to death or percentage of deaths. In all cases the equal rate lines were portions of parallel ellipses. Taylor (1927) developed a diagram of percentage of infant mortality in relation to rainfall. It consisted of several ellipses tilted in an unusual direction.

No one has been successful in relating variations in populations to temperature and humidity when related to each other as in the thermohygrograms. Populations appear to be controlled in some other

way. It will, however, be shown that similar diagrams can be developed for population size if the correct factors are selected.

III. ECOLOGICAL TYPES OF POPULATION

The animal populations of the Trelease Woods fall into two main ecological groups: (1) the forest population of both vertebrates and invertebrates which breeds in the woods and does not ordinarily leave wooded areas, (2) the non-forest population which is made up of (a) species of invertebrates which come into the forest in September and October or earlier, hibernate in the litter or soil, and return to breed in the forest-edge and fields of grasslands, principally in April and May, and (b) species of vertebrates considered herein which breed in the forest-edge and enter the woods for shelter in winter.

Occasionally non-forest invertebrates are found in the herb and shrub levels in late August, which represents the beginning of hibernation migrations (Fig. 2). Thus migration does not appear to be influenced by temperature. Figure 2 shows only the herb-shrub net collections made weekly as the animals are preparing to go into and come out of hibernation, 1934 through 1940. Consistency between fall and spring cannot be expected without daily collections. A group may arrive in the woods and enter the litter so quickly as to be missed by weekly or fortnightly collections. Nevertheless, winter losses are suggested. As a rule a comparison of the sum of individuals from September, October, and November with that of April, May, and June shows winter shrinkage of non-forest populations. In autumn the non-forest species come into the woods and move downward from the shrubs to the herbs to the ground largely without regard to weather. In the spring their return to the plants is controlled by weather (Weese 1924). The general decline of both forest and non-forest populations is suggested by the autumns of 1937 through 1940.

The forest invertebrates with populations easily studied are millipeds, spiders, insects and mollusks which will be treated in a later paper. The forest birds and mammals constitute two different ecological types. The small resident birds, reported by Kendeigh (1944, 1948), are exposed to the atmosphere chiefly without protection. They differ from the squirrel, which spends much of its time in winter in hollow trees and in summer in nests of its own building. The response of the two groups to environmental conditions as evidenced by a difference in the time of their peaks of abundance, is not the same.

Taken as a whole, including forest and non-forest, vertebrates and invertebrates, the populations evi-

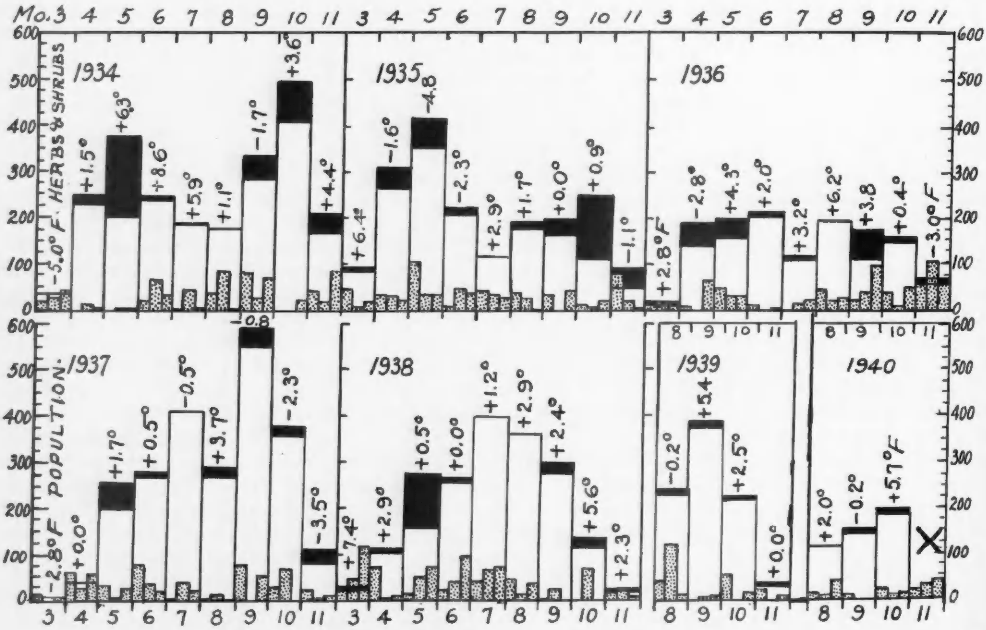

FIG. 2. Histogram for the comparison of changes in forest and non-forest population on the herbs and shrubs of Trelease Woods in 1934 through 1940, with temperature and rainfall data. The forest population is shown in white and the non-forest in black. One unit on the vertical scale equals 25 individuals per m.[2] The rainfall is shown by stippled areas representing approximate ten-day periods, and one unit on the scale equals one inch or approximately 25 mm of rain. The deviation from normal temperature is shown above the histogram for each month in °F. X indicates no data. Compare March-April in 1934 and 1937 with corresponding months in 1935 and 1938. Note decline in non-forest herb-shrub population 1937 through 1940. Compare year to year increases and decreases of forest herb-shrub populations with the spider graph and non-forest with the chinch bug graph in Fig. 3.

dently fall into four types through their response to physical conditions. Figure 3 shows curves of four population types below a curve for the total number of sunspot groups observed yearly 1932-1948. The figure is intended to illustrate the application of narrow limits of physical conditions in influencing populations, although such conditions are not directly indicated by the sunspot curve.

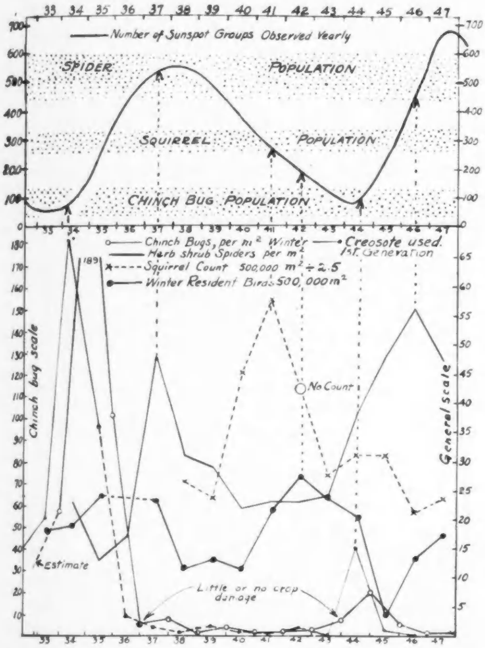

FIG. 3. The sunspot group curve is shown above the four types of populations; the chinch bug, typical of non-forest invertebrates; spiders, of forest inverterates; and fox squirrel, 40% of actual count, of forest vertebrates and small birds. The stippled bands indicate suggested intensity toleration limits or optimum of some kind of solar phenomena probably associated with total number of sunspot groups (Baker, 1946). The bird tolerance band is not added because of the absence of 1936 data. The size of the first new annual chinch bug generation population (commonly called second generation) is based on the number of gallons of control creosote used in Champaign Co. divided by 4,000, which gave an arbitrary maximum of 177 for the first new generation in 1934; the average monthly count (October through May per m²) for the overwintering (1934-1935) generation was 189 chinch bugs. For the 1944 maximum, the first new generation arbitrary creosote figure was 41 and for counts of the overwintering (1944-1945) generation, 20. The curve for the first generation is a broken line where estimates were used. No direct relation between sunspots and these populations is assumed; the indirect relation of the sunspots and population is discussed on page 165.

The first large peak is indicated by two chinch bug curves with the maxima at the left representing two generations in one year, which must be considered together. The tendencies of the non-forest population is illustrated by the chinch bug, which has large populations and responds sharply. The first curve, plotted on the center of the space for each year, is based largely upon the amount of chinch bug control creosote used from year to year in Champaign Co. in which the Trelease Woods is centrally located. The second curve represents the population of chinch bugs found in the woods in the autumn and winter following the hibernation migration. The large populations appeared just as sunspots had passed the minimum and started to increase.

The second probable large peak represents four species of resident birds: cardinal, downy woodpecker, tufted titmouse, and white-breasted nuthatch.

The third large peak represents a distinct forest group, the spiders that inhabit the herbs and shrubs. The peaks of this population came nearly at the maximum of sunspots and related phenomena.

The fourth large peak, representing the fox squirrel population, came when the solar phenomena were approaching a minimum.

Figure 3 shows the following series of maxima and minima:

	Min.	Max.	Min.	Max.	Min.
Chinch bug ......(Fig. 11,	1929)	(1934)	1938*	1944	1946
Birds	1933	1936	1939	1942	1945
Spiders	1935	1937	1940	1946	......
Squirrels	....	....	1939	1941	1946

*Champaign Co.

In Fig. 3 the relations to the level of sunspot groups is indicated for the several maxima. The population stimulus if finally traceable to solar activity must of necessity be to phenomena not in complete correlation with sunspots either chronologically or quantitatively. However, Figure 3 is drawn to suggest the operation of an optimal quantity. Figure 3 appears to illustrate this in an unusual manner, but over any considerable period of years only the forest (e.g., spiders) and non-forest (e.g., chinch bug) invertebrates can be expected to show similar relations. The known relations of the others cover too short a period.

For considering the relations of populations to weather conditions, the precipitation records at the Urbana Weather Station have been plotted above population curves covering the fourteen years with two earlier years for the chinch bug (Fig. 4). The rainfall data for each year, for March through October, and for March through June, etc., are shown. There is little consistency in the relations between populations and the actual level of rainfall. Nevertheless, it is obvious that the rainfall for the year, and for the several periods, show a general upward trend through the 17-year period. The forest population shows a higher peak in 1945-47 than in 1937-39. Still more striking is the decline in the non-forest populations over the same period. The second (1944) peak of non-forest populations is only one-third or less of the first (1934). That snowfall and percent of possible sunshine indicate no consistent relations with population is obvious in Fig. 4. The populations were checked against single and combined monthly temperatures but no correlations were evident.

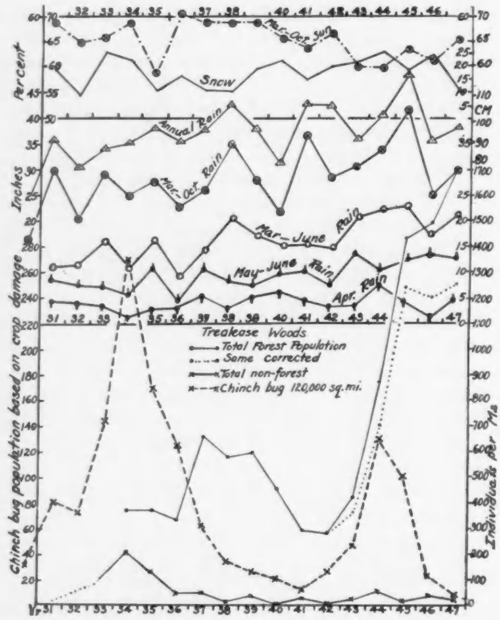

FIG. 4. The lower section concerns populations: (a) the total population average per m², May through October, of forest-inhabiting invertebrates. The 1947 population as shown is much larger than the 1937 population. The dotted corrected curve for 1943-47 is presented for the following reasons. In the 1943-47 period large numbers of immature millipeds were followed by a very large number of small staplylinids, etc. They were present in insignificant numbers until 1943 and neither group was counted until that date; their numbers observed in 1943-47 were deducted from totals to give figures represented by the corrected curve.

(b) The non-forest population of the woods including chinch bugs, shown on the same scale—maxima 1934 and 1944 plotted on the year beginning in August or September when the majority enter the woods and ending in spring when numbers reach a minimum. Both the forest and non-forest species increased in both 1943 and 1944. This probably results from the peculiar distribution of the precipitation.

(c) The chinch bug population curve is from the data of Shelford & Flint (1943) with the 1944-47 data added. The arbitrary scale (1.7 times the scale in Fig. 9) represents relative crop damage and not the enormous difference in numbers of individuals.

The two top sections; graphs of weather conditions at the Urbana Station (only roughly applicable to the 120,000 sq. mi. of Shelford & Flint 1943). Correlations of population size are least often with annual rainfall and most often wtih one of the three spring periods graphed.

IV. THE NON-FOREST SPECIES

All the strictly non-forest species considered here are invertebrates. They include among other less abundant species the following: tarnished plant bug, *Lygus oblineatus* (Say); chinch bug, *Blissus leucopterus* (Say); striped cucumber beetle, *Diabrotica vittata* (Fabr.); 12-spotted cucumber beetle, *D. 12-punctata* (Fabr.) (not strictly non-forest); egg-plant beetle, *Epitrix fuscula* Cr.; the horned thorax beetles, *Notoxus monodon* Fabr., and *Notoxus bicolor* Say. Horned thorax beetles are forest-edge inhabitants, unformly most abundant in forest samples in fall and spring. The populations of all these species were deducted from the total and the resulting figures are used as the total population of woods species (Carpenter 1935, Rutherford 1929).

Weese had a larger list of non-forest species. He classified the following beetles as breeding in the forest-edge: *Chaetocnema confinis* Crot., *Phyllotreta sinuata* (Steph.); *Longitarsus melanurus* Melch.; and the European weevil, *Phytonomus nigrirostris* (Fabr.). The last species has been taken in the woods in summer. He also classified the hemipteran, *Corimelaena pulicaria* (Germ.), as a forest-edge species. The woodland area is too small to exclude forest-edge species which are within easy distance of openings caused by fallen trees, etc. Such scattered individuals of the five species listed will be included with the woods population in a later paper. They are not present or are very few in numbers, except possibly in very dry periods, and were insignificant in the total forest population.

In addition to the invertebrates, the cottontail, *Sylvilagus floridanus mearnsi* (Allen), and quail, *Colinus virginianus* (Linn.), occur in the the forest-edge along with a score of small birds. My colleagues have accumulated some records of all of these, but only a few of the quail.

The non-forest invertebrates while on the vegetation were sampled along with the forest population by 48 strokes of a 13 inch (30 cm) net. After they entered the litter they were removed from two to four one-tenth m² samples per month for five or six months of autumn, winter, and spring.

The general conditions of the aggregate populations have been discussed. Fig. 5 shows the population indices of four species. The graph of *Epitrix fuscula* is omitted because it appeared that individuals of this species were not all removed from the samples; the numbers recovered from samples are, however, included in the non-forest total. The chinch bug is omitted because it will be especially treated later and has been shown separately in Figs. 3 and 4. It is notable that the five species graphed had large populations produced in 1933 through 1935. All had declined sharply by 1937-38. In 1947 and 1948 there was no crop damage for any of the non-forest species in Champaign Co. In the winter of 1948 collections were made at the south side of Brownfield Woods, which can be compared with the records of 1934. Brownfield Woods is approximately one mile northwest of Trelease Woods, contains about ten acres more of virgin forest, and is better drained. Its south side is bounded by a dirt road which makes possible the demonstration of the normal responses of non-forest species. For many years records were kept from a class of graduate students (Table 1). As a rule the non-forest insects are not abundant beyond 30 m from a woods edge. Beyond 30 m, they are generally present in small numbers.

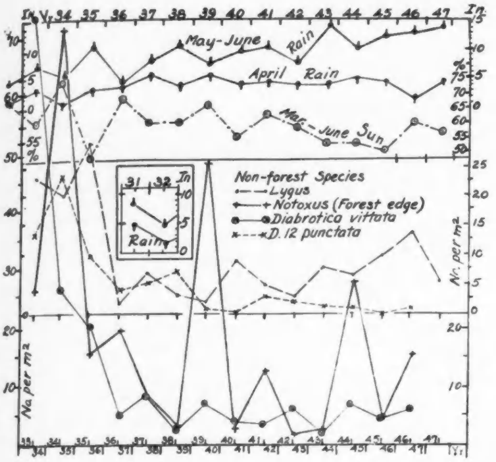

FIG. 5. Weather conditions affecting forest populations and the graphs of populations of five non-forest species.

Average number of specimens collected per m² per month; Notoxus and *Diabrotica vittata* for 10 months, Lygus for 7 months and *Diabrotica 12-punctata* total specimens taken per year per m². Note April rain and percentage of possible sunshine, especially 1931 through 1935; the percentage possible sunshine for 1931 was 60% and for 1932, 67%.

TABLE 1. Showing the population of chinch bugs, tarnished plant bugs and Notoxus in the winters of 1934-35 and 1948-49 in Brownfield Woods. * present. Figures indicate individuals per m².

Distance from So. Edge in m	Year	0	1	10	30	310
Chinch Bugs	1934-35	775	3500	2030	2107	43
	1948-49	5	2	2	0	—
Tarnished Plant Bug	1934-35	*	*	17	*	7
	1948-49	0	10	1	4	*
Notoxus	1948-49	0	0	8	4	*

The collections have been made in Trelease Woods 100 m from the west margin of the woods and 400 m from the south edge. The decline in numbers of chinch bugs toward the interior of Brownfield Woods is noteworthy. The tarnished plant bug goes well into the interior but also with declining numbers. This no doubt has influenced the size of the collections unfavorably. The study is being continued and this defect will be remedied by annual collections.

After 1936 the collection of the two cucumber beetles were so small that all specimens taken from September through August were used to make the graph. *Diabrotica 12-punctata* was especially low after 1938. It is more clearly a grassland species than *D. vittata.* Both of these species have two generations and all life history stages may be found at one time. It will be best to leave these until there is another larger increase.

Notoxus is supposed to have but one generation. The large increases in 1939 and in 1944 are difficult to explain.

Lygus oblineatus (Say) shows a population sufficient to permit analysis. There are two generations each summer. It requires or tolerates more rainfall than the chinch bug. The population declined in 1934 when chinch bugs were most abundant. The population was largest in 1935 when the chinch bug declined.

Figure 6A shows the months with least variation in rainfall and temperature in the years (1935, 1937, 1940, 1943, 1945, and 1946) in which the Lygus population increased. As has been pointed out, it has been shown (Johnson 1924) that months which are favorable to an organism as shown by population increase, etc., fall within narrow limits from favorable year to favorable year. Johnson's sheep study was concerned with survival and related matters. These months represent sensitive periods in the life history. In this case (Fig. 6A) the sensitive months would be April and July. These are the months in which eggs and young nymphs occur, and survival and not fecundity is involved. A similar diagram of rainfall and sunshine (Fig. 6C) shows March and June have narrowest limits. This limited case cannot be relied upon. Furthermore, the differences are not great and the results not easily figured due to much overlapping of areas. When the months of April and July are combined, using mean percentage of possible sunshine and the rainfall sum, a heliohydrogram cannot be drawn with population size as a basis. However, Fig. 6B shows that when sunshine and rainfall, March through August, are used, years with increases fall between 57% and 67% possible sushine, while there appears to be little correlation with rainfall.

V. THE CHINCH BUG

The chinch bug is a species with its original center of population in Illinois, northeastern Missouri, and eastern Iowa. This was the basis for selecting the 120,000 sq. mi. area used by Shelford & Flint (1943). The area would have extended farther west but early records were wanting; however, it advantageously omitted areas of heavy winter killing (Decker & Andre 1936). The insect does not feed primarily on the climax grasses but on annual grasses in waste places and so its food proclivity was readily transferred to crops. Its range was extended westward with the introduction of grass and other crops.

The rather striking separation of the large populations of non-forest species and the chinch bug from the other groups shown in Fig. 3 gives them an importance not anticipated when it was originally planned to emphasize only the forest species. There are records of outbreaks dating back to 1823 and reliable records 1870 to date. It has been a subject of several intensive studies. Thomas (1879) covered meteorological conditions, 1840 to 1878. Forbes (1916) made a detailed study of the 1910-16 southern Illinois outbreak. The writer's (Shelford 1932)

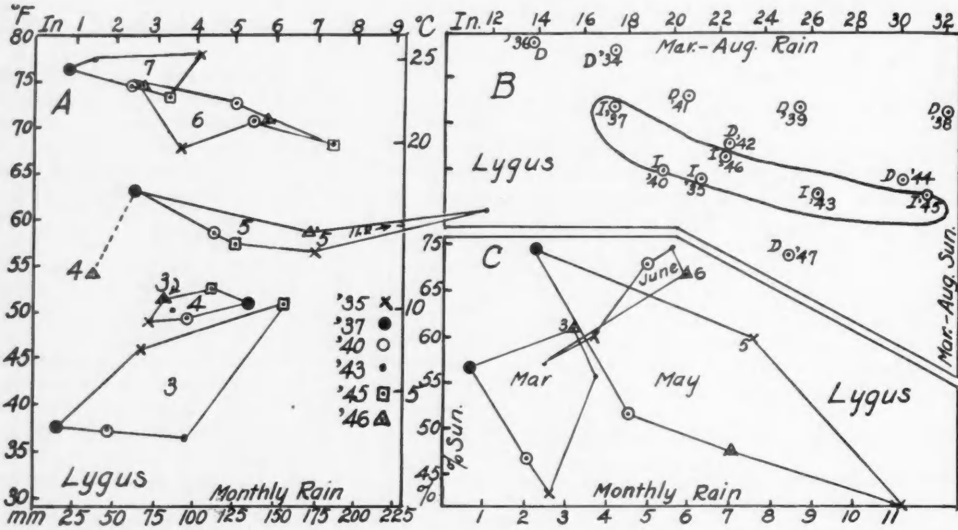

FIG. 6. A. The least variation in temperature and humidity for 6 years in which the Lygus population increased falls in April and July, the principal months of reproductive activity. March 1946 was so much warmer than the average that it is considered April and April is considered with May. B. The location of increases (I) and decreases (D) of population with respect to March through August total rainfall and average percent possible sunshine. The two-digit figures refer to years. C. The months of least variation for the five years of largest increase, for rainfall and sunshine. March and June had smallest limits; more months cannot be easily represented; the month before actual egg laying appears to be the month of stimulation by solar radiation.

experimental study (1916-1925) provided a thermohygrogram of each of the life history stages and of the life history from egg to adult and noted sharp differences in vigor from year to year. Dahms (1947) has shown that fecundity and other physiological conditions are modified by food.

Seven years of additional data have accumulated since 1940. Recorded amounts of creosote were used to repel and trap chinch bugs. The amounts used from year to year are the best indicators of bug population available and were used to draw one curve of chinch bug population in Champaign Co. which surrounds Trelease Woods, shown in Fig. 3; the population is estimated where the curve is a broken line (see acknowledgments).

Much dependence has been placed on rainfall as almost the sole control of chinch bug population. Pest control entomologists are, however, by the nature of their work, little interested in pests (a) when populations are small, (b) when they fail to increase and do damage though conditions are favorable, and (c) in the case of the chinch bug when May-June rainfall fails to check them, which occasionally happens.

1. Rainfall

The first step in testing new factors such as solar phenomena is to make a thorough study of rainfall relations. Statistical boundaries between years favorable and years unfavorable to the development of crop-damaging populations must be established. The rainfall records available for the 120,000 square miles of Shelford & Flint (1943) were used by counties. All data from counties without weather stations are omitted. More than 5,000 monthly rainfall records were examined along with 2,000 temperature records. Primary emphasis of practical entomologists has been on the May-June rainfall. August rainfall has been regarded as important in some cases (Forbes 1916).

A. August Rainfall

It is a common belief that low August rainfall is favorable to nymph survival, which increases population the following year. Forbes (1916) expressed the view that the hot-dry conditions in August, 1909, started the 1910-16 southern Illinois large outbreak. There are, however, no comparative quantitative data as to bug population in July, 1909, in September, 1909, and in late April, 1910. Forbes' conclusions are evidently based on the amount of damage in 1910.

The data on the Augusts preceding population declines and increases the following year were broken down into rainfall classes and percent of increase. The remainder of the 100% represents decreases determined as follows:

Under 3.3 in.,	719 cases;	53% increases
3.3 to 4.0 in.,	260 cases;	45% increases
4.0 to 6.0 in.,	254 cases;	43% increases
6.0 to 10 in.,	127 cases;	48% increases
Above 10 in.,	27 cases;	55% increases

There were 334 cases in which the damage is rated as the same as that of the preceding year. It is evident that August rainfall is not usually of great importance.

B. MAY-JUNE RAINFALL

The question as to which is more favorable to the chinch bug, years in which rainfall is higher in May than in June or years in which rainfall is higher in June than in May, was explored. Increases and decreases in chinch bug population were recorded. Increases in chinch bug populations occurred in 51% of 644 cases in which precipitation was higher in May than in June, and in 46% of 604 cases in which rainfall was higher in June than in May. These figures probably reflect the late progress of some seasons, which may throw the maximum number of small nymphs into June rather than May. In general it makes little or no difference to chinch bugs which month has the more rain. The average rainfall for the entire state of Illinois for 20-year periods using all records, varies. The 20-year averages for 1887 to 1907 are: May, 4.00 in.; June, 4.09 in.; for 1907 to 1927: May, 4.01 in.; June, 3.90 in.; for 1927 to 1947: May, 4.16 in.; June, 4.02 in. Illinois stations are representative of the 120,000 square mile area. Average years appear to be favorable to chinch bugs but are of rare occurrence.

To determine the general effect on chinch bug populations of varying amounts of May and June precipitation, the following categories were used as applied to both May and June: under 5.0 in.; 5.0 to 5.5 in.; and more than 5.5 in.

Less than 5.0 in.,	May,	1209 cases;	47% increases
Less than 5.0 in.,	June,	1106 cases;	62% increases
5.0 to 5.5 in.,	May,	109 cases;	50% increases
5.0 to 5.5 in.,	June,	148 cases;	44% increases
More than 5.5 in.,	May,	478 cases;	41% increases
More than 5.5 in.,	June,	387 cases;	39% increases

C. TOTAL MAY-JUNE RAINFALL

Since it makes little difference to chinch bug populations whether May or June has the more rain, it was assumed that the total for the two months may be safely used. To test this conclusion, the following categories were used: under 10.0 in.; 10.0 to 10.5 in.; more than 10.5 in.

Under 10 in.,	1189 cases;	57% increases
10.0 to 10.5 in.	69 cases;	59% increases
More than 10.5 in.,	453 cases;	38% increases

From this and Figure 11, it was concluded that 9.5 inches is the upper limit except when the bugs possess unusual vigor. The use of a creosote index of chinch bug population has been discussed for Champaign Co. A record of the amount used in Illinois and adjoining states, 1940 through 1947, was made available by Mr. Claude Wakeland, Chief of U. S. Bureau of Entomology and Plant Quarantine Division of Grasshopper Control. There are two uses that may be made of these data: (a) the amount of creosote used may be regarded as an index of population and changes in population only in case where consecutive years of use may be utilized; (b) the amount of creosote used in the entire state may be considered as indicative of the general population. In the case of the Shelford & Flint (1943, p. 451) estimates the crop damage was mapped as severe and slight by counties and parts of counties. The amount of creosote used in a county has a direct relation to its area, so definite comparison can be made from year to year. Large area estimates are on the basis of the sum of weighted unit areas or counties. The Trelease Woods collection records are merely population per unit area, the square meter.

There are 112 county-years of creosote records for Illinois in the period 1942 to 1946. There was an increase in May-June precipitation over the preceding year, roughly 1 in. in 1941; 2 in. in 1942; and 4 in. in 1943. Sixty county-years were characterized by bug damage and creosote use in the preceding year. Of these, 32 (53%) showed decreases in bug population accompanying increases in precipitation. Thirteen (22%) represented increases in 1944 accompanying declines in rainfall from 13 in. to an average of 6 in. Fifteen (25%) of the county-years showed either increases or the same condition accompanying increases in rainfall noted above. This is a high percentage to accompany increased rainfall. May-June totals associated with the increases were as follows: 11.88 in., 13.51 in., 17.43 in., 13.38 in., 17.25 in., 10.88 in., 10.52, 10.50, and 12.26 in. The rather poor correlation of population with rainfall indicates that amount of precipitation is not fundamental in the case of some outbreaks at least.

This is further emphasized by the conditions in Missouri 1943-1947. There was a severe outbreak in seven counties in the northeastern part of the state in 1943 with the May-June rainfall ranging from 11.00 to 17.45 in. In 1945 there was damage in a considerable area with May-June rainfall ranging from 10.00 to 16.38 in. in twenty-eight cases.

In their 1943 paper, Shelford & Flint stressed the spottiness of rainfall as a factor in controlling local populations of chinch bugs and it is still important in many cases. With the discovery that the combined May and June rainfall is as good an index as the months taken separately, it was also found that combining these two months greatly reduces the apparent spottiness. Furthermore, the extensive examination of weather data associated with increased populations has increased the estimated upper limits of toleration of rainfall. The upper statistical limits of 5.5 to 6.0 in. for May and June combined (Shelford 1932) are raised to 8.0 to 9.5 in. Weather data and population distribution indicate that only 4% to 6% of the peculiar records are due to spottiness of rainfall. Furthermore, high wind during rains may destroy many nymphs with a comparatively small total precipitation.

The climographs and limits of critical months (Shelford 1932) were disappointing. Fig. 7 shows four climographs without characteristics which distinguish years of increase from sharp decrease. Fig. 7A shows weather for a good year (1922-23) for chinch bugs at La Harpe, Illinois, and a supposed "bad" year at Philo, Illinois, in which the population increased from one doing no damage to one doing moderately severe damage. In 1887-1888, Fig. 7B, May and June rainfall exceeded 12 in. and the diagram is typical of rainfall conditions of the state.

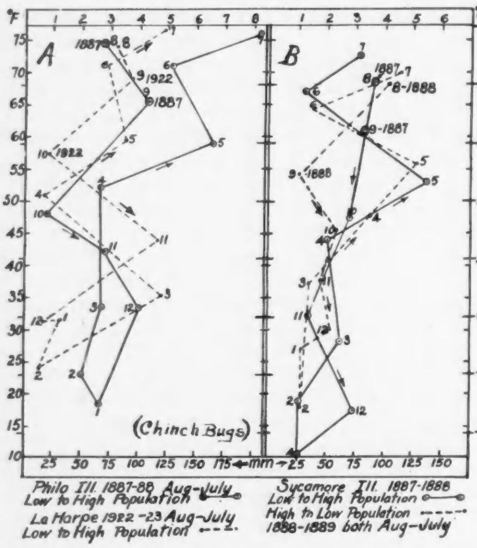

FIG. 7. Climographs based on monthly data August through July showing the failure of weather to control chinch bug populations. In the left half of the figure there were chinch bug population increases when rainfall was large in Philo and small at La Harpe. In the right half, the solid line climograph shows (1887-88) a year of large chinch bug population increase and the broken line climograph (1888-89) a year of very much larger population decrease, although the two resemble each other very closely.

The two Sycamore, Illinois, climographs are almost identical as to May-June and August conditions, one representing a year of moderately severe damage and the other showing a year of almost complete collapse of the population.

Because of the ineffectiveness of the ordinary climographs based on months, the months of April, May, and June, which are critical months in this study, were divided in 15 or 16 day periods. This division was useful, but after 25 or 30 trials with these they were abandoned and 10-day climographs were used (Fig. 8, A to E).

Few day-to-day records of temperature or rainfall are available during the early chinch bug outbreaks; some are available for 1888 and a few more for 1889. Figure 8A, Champaign Co., shows typical conditions in Illinois in 1888, a year that according to all criteria was unfavorable for chinch bug populations. It was, however, one in which there was a large population of bugs over the 120,000 square mile area and in Champaign Co. There were three ten-day periods with heavy rain about the time young chinch bugs were probably present. All the 1888 ten-day diagrams that could be made were similar to that for Champaign Co. The weather of 1889 was similar to that of 1888. Some of the ten-day diagrams indicate better chinch bug conditions in 1889 than in 1888, yet the sharp decline was in 1889 (see Fig. 11, p. 166).

Climographs on a ten-day basis were prepared for a large number of years for Urbana, Illinois, and several other stations. The climographs for 1925, 1926, and 1936 are based upon records of the Decatur weather station in Macon Co., Illinois, 50 miles southwest of Urbana, used because Macon Co. was near the center of the chinch bug infested area during most of the period, especially 1927 through 1936. In 1925 and 1926, the damaging chinch bug population was in Christian Co., 30 miles southwest of Decatur. The 10-day climographs were essentially the same for stations in the infested county as in the Urbana and Decatur areas, which had a very small population. This points to an additional factor as having important effects.

2. RELATIONS TO TEMPERATURE

Thomas (1879) stated that two or three favorable years are necessary for a crop-damaging population of chinch bugs to develop. The more important outbreaks (see Fig. 11, p. 166, herein) have been preceded by one to three years of high temperature. The large outbreaks of 1871-75 were preceded by high temperature, likewise those of 1881-83, 1886-89, 1910-16, 1922-24, 1933-37, and 1942-46, which means primarily that temperatures are higher in the Mississippi Valley before and after the sunspot peak (see Fig. 11). These differences of approximately 10° F. (5.6° C.) between the April and May temperatures of different years can probably effect changes only by increasing the rate of development. Increased rate of development reduces all hazards to the young nymphs by shortening the length of sensitive instars so that more progress is made between heavy showers and hazards from predators (if any) are reduced. The development of the early stages of the chinch bug begins at about 59° F. (15° C.), increases rapidly with increase in temperature to 67° F. (19° C.), then increases in direct proportion to the increase in temperature to 85° F. (29° C.). Above 85° F. the rate begins to decline with increased temperature more rapidly than it increased at lower temperatures (Shelford 1932). These are specific hereditary characters (Shelford 1929a and citations). Thus either too high or too low temperatures retard development regardless of geographic location. The mean of maxima at Cairo, in extreme southern Illinois for May is 76° F. (24° C.) while at Rockford, in extreme northern Illinois, it is 70° F. (21° C.), and for June, Cairo, 84° F. (29° C.); Rockford, 79° F. (26° C.). The apparent geographic optimum of average daily maxima and minima during the development of the early stages lies at about 39° N. Lat. and east of St. Louis, Missouri. The advantage of the higher temperature which may have accompanied outbreaks has probably tended to cause the bugs to extend northward more often than southward. The differences in combined May-June rainfall at Rockford and at Cairo are small. Both average approximately 7.5 in. (19 cm).

3. CRITERIA FOR FAVORABLE CHINCH BUG YEARS

April, May and June were broken down into ten-day periods for years favorable to the chinch bug. The year 1934 was used as one type of model (Fig. 8C). The lowest temperature at which development takes place is about 59° F. (Shelford 1932). The temperature at which changes in the gonads take place is not known but is probably about 60° F. (15.6° C.). Locomotion and flight take place at about 70° F. (21° C.). For variation in period between leaving hibernation and egg-laying, see page 163.

An inspection of daily weather records in 10-day periods with mean temperature of 70° F. shows that the maxima will range from 65-90° F. and about half of the minima will be above 60° F. A mean of 70° F. or above gives rapid development. With a mean of 65° F. the maxima usually range from 63° to 86° F. and two or more of the minima will be above the 60° F. With a mean of 60° the lowest maximum is likely to be 60° and the highest 80°. With a mean of 55° F. more than half of the days in a 10-day period will be above 60° F. for a considerable part of the hours from sunrise to sunset. With a mean of 45° F. about one-third of the days will have a maximum above 60° F.; these temperaatures are of short duration and material objects do not have time to warm to above 60° F.

The criteria for favorable years for chinch bug eggs and nymphs used in this study are the following:

(1) Favorable April, May and June ten-day periods.
 (a) Three ten-day periods with mean temperature of 60° F. (15.6° C.) or above and not more than a total of 1.00 in. of rain; less than 1.00 in. in all 10-day periods, or
 (b) Four ten-day periods with mean of 55° F.

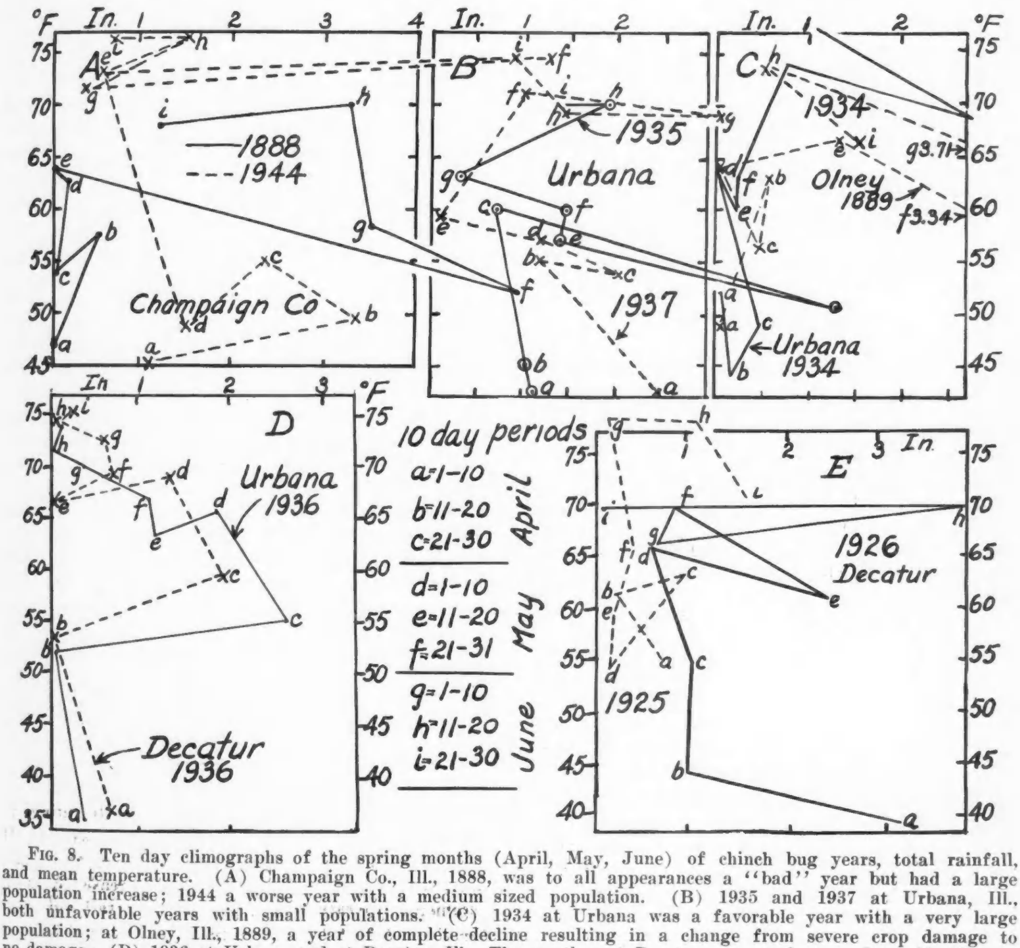

FIG. 8. Ten day climographs of the spring months (April, May, June) of chinch bug years, total rainfall, and mean temperature. (A) Champaign Co., Ill., 1888, was to all appearances a "bad" year but had a large population increase; 1944 a worse year with a medium sized population. (B) 1935 and 1937 at Urbana, Ill., both unfavorable years with small populations. (C) 1934 at Urbana was a favorable year with a very large population; at Olney, Ill., 1889, a year of complete decline resulting in a change from severe crop damage to no damage. (D) 1936 at Urbana and at Decatur, Ill. The weather at Decatur was much more favorable than at Urbana, with higher temperatures and less rainfall in late May and early June accompanying a larger population. (E) 1925 and 1926 at Decatur where 1925 was a favorable year with a decline in population; 1926 was an unfavorable year with a small increase in population.

(12.8° C.) or above, or five ten-day periods with above 50°. Total rainfall limits increased in proportion to length of the period.
(2) Combined May and June rainfall less than 9.5 in.

Attention must be given to the August rainfall of the year preceding the population of the year under consideration. The second generation nymphs hatch in August and these nymphs produce the adults which pass the winter. The August weather is more uniform from year to year than that of the spring months. The spread of egg laying is usually greater than in the spring so that particular storms have less chance of reducing the population.

In evaluating weather with reference to the criteria enumerated, supplementary attention must be given to (a) the time at which the heavy rainfall occurs and to rains of cloud burst character; (b) the occurrence of temperatures that will bring insects out of hibernation; (c) the favorable or unfavorable character of the preceding August with reference to overwintering populations; (d) unusual warm weather in March; (e) the occurrence of disease, especially the growth of fungus on the bodies of the bugs.

A spring period in which warm weather with little rain occurs early, enabling eggs to be deposited and young nymphs to hatch in great numbers, followed by heavy rains, may cause decreases in population. The probable date at which heavy rains can do most damage will vary from the last week of May to the second week of June. There is a lack of quantitative data on numbers of nymphs and too little field knowledge of life histories. Nymphs may begin hatching early in May, or hatching may be delayed until late in June, dependent in part on latitude.

Fungus attacks occur only when much rain, high humidity, and abnormally low temperature occur together. Decker (1945, and personal communication) stated in his 1945 report, which is filed but not printed, that between June 15 and June 20 fully 75% of the adult overwintered chinch bugs in central Illinois were destroyed by an epidemic of fungus disease. The epidemic came at a time when oviposition, which was late, had not as yet reached a peak, and had a great influence on the chinch bug populations of that year (Billings & Glenn 1911).

4. Overlooked Conditions

May-June precipitation has been depended upon in prediction of possible chinch bug damage, and this practice has been followed with little analysis as to details. Little notice has been taken of (a) occasional failures of heavy rain to check chinch bug outbreaks, or (b) the failure of populations to develop under favorable conditions over considerable periods. No comment on the absence of chinch bug damage 1898 through 1903 and 1905 through 1908 has been found. There was a slight damage southeast of St. Louis in Washington Co., Illinois, in 1904 which did not continue in 1905. Several periods of two or three years were favorable in local areas and near the area of the 1904 damage. Eleven counties had three or more favorable years between 1900 and 1906. The accuracy of the record is marred by (a) lack of information as to the size of chinch bug populations when no crop damage is reported and (b) lack of knowledge as to variation within the categories "severe damage," "moderate damage," and "slight damage." Greater accuracy was achieved, 1941-1946, in Illinois by using the creosote record.

5. The Creosote Index of Population

The creosote record covers Illinois throughout this period 1934-1946 with some records missing and includes Missouri, Iowa, and Indiana, for 1941 and 1942, the only years in which records from these states were available. Thousands of gallons of creosote used per county gives a series of values for the lesser infestations not available by other methods and in better accord with the actual population. The scales used in the Champaign Co. graph for the damaging population in Fig. 3 is gallons of creosote divided by 4000, which was used as a general guide throughout the study. The chinch bug population from 1923 through 1947 was harmonized with the record of Shelford & Flint (1943, p. 451). The creosote record was wanting in several years 1936 through 1939 and estimates were substituted. One error was found in the Shelford & Flint graph on p. 451; in the year 1936 the population was actually considerably lower than in 1935. A map of overwintering population was accidentally substituted for the damage map.

The 1940-1947 creosote period indicated that the large populations arose from the local populations. There is not a suggestion in the infestation maps indicating that the vigorous population spread from one center. On the contrary, the indication is that the local population increased and declined from year to year in a spotty manner over a wide area. New isolated slight damage appeared for one year separated by 50 to 100 miles from any other area. No single county was continuously infested throughout the entire period and in only two or three cases did the infestation appear to be the same in two consecutive years. The wide and variable range of rainfall tolerated in different years and different outbreaks in the creosote control study emphasizes the varying hardiness of the breeding adults and young nymphs, even though it is admitted that more nymphs may survive when a population is very large than when it is somewhat smaller.

6. Variation in the Vigor of Bugs and Population Behavior

After thirty years' experience in attempting to control the chinch bug, Forbes (1916) wrote: "It must be admitted, however, that proof of the immediate dependence of chinch bug increase on high summer temperatures and moderate rainfall and upon the character of the agricultural crops is not here so clean cut and positive as to put the conclusion altogether beyond question." In the study in question, Forbes expressed the belief that the population was

blown during flight periods toward the northeast from a point near St. Louis. This assumes that there were no virile bugs in the area. In the writer's 36 years of animal collecting with classes in and south of Champaign Co., chinch bugs, so far as can be ascertained, have always been present within their regular range which includes Champaign Co., but were scarce at times. The numbers found when they are not of epidemic proportions are comparable to populations of other species associated with them, as shown in Table 1, p. 157. Only a few of the outbreaks can easily be interpreted to have started at one point and spread to surrounding areas, for example those in 1909 to 1914 and 1929 to 1939 (Shelford & Flint 1943).

Experiments with insecticides have shown the chinch bugs are sometimes very weak at the time of leaving hibernation. This was true at Coulterville, Illinois, in 1913 when oil emulsion sprays were found to kill bugs, but a check showed water to be equally effective. In 1916 through 1923 there was serious difficulty in over-wintering the adults in refrigerators or out-of-doors; so the efforts were abandoned. In Iowa in 1932-35 there was no difficulty in carrying adults through the winter and finding them vigorous in the spring. Shelford (1932) pointed out sharp variations in vigor, and his observations were summarized by Shelford & Flint (1943). The difference in reproductive vigor in the weak 1921 cultures as compared with the strong 1925 bugs amounts to nearly 200-fold. Furthermore, the great variation in the amount of rainfall tolerated suggests chiefly that the vigor of the young nymphs varies greatly or the number produced is excessively large at times so that the losses do not reduced the damage-causing population appreciably. Likewise the application of control measures is very destructive to populations and yet does not appear to reduce the large population the following year.

The number of eggs laid by chinch bugs varies from time to time. The eggs are well hidden away and not usually parasitized, and probably, under fairly favorable conditions, nearly all hatch and are deposited in several lots distributed over a month or more. There are frequent copulations during the egg-laying period. The population may increase fairly rapidly but with a minimal population more than one favorable year will normally be required for a population to reach a crop damaging level (Thomas 1879). Forbes (1905) gives average eggs laid.

Shimer (1867) gives an excellent account of a chinch bug life history and the great abundance of the insects. The work of Johnson (Forbes 1894) and Janes (1937), made important contributions. The egg-laying records are as follows:

Shimer (1867), females laid 500 eggs (northwestern Illinois, 1865).

Johnson (1894), second generation females, 98 to 137 eggs, average 164. Life of females, 48 to 53 days (Champaign, Ill.).

Janes (1937), second generation females (1934), 495 eggs; overwintered females, 544 eggs; one individual, 1091 eggs, oviposition period, 25 to 110 days. End of hibernation to egg laying, 2 to 12 days (Iowa).

In Kansas in 1912, Headlee & McColloch (1913) state that three weeks intervene between flight from hibernation and egg-laying. Unfortunately there is little comparable data from outbreak to outbreak. The difference in reproductive vigor is evidently one of the chief causes of the sudden increases in population. The data lose some of their force, however, because of lack of comparisons with periods of low population.

VI. CHINCH BUG POPULATIONS IN RELATION TO THE WEATHER AND SOLAR RECORD 1823 THROUGH 1947

The decline of the 1919-24 chinch bug outbreak coincides with the beginning of Pettit's (1932 & I.A.U.) ultraviolet measurements and Figure 1 (p. 151) should be consulted. The changes in non-forest population types may be followed in Figure 9. Here the ultraviolet data have been adapted to the early spring flights and other movements of the chinch bug. The records of daily temperature were examined with reference to radiant energy. In two cases April readings were omitted because there were no temperatures that would bring the insects into flight from the hibernation quarters to the grain fields or grasses.

Figure 9 principally covers the period 1923 through 1944 and shows populations of chinch bugs and other non-forest species. It is laid out to illustrate the idea of optimum intensities of a factor. The average May-June rainfall for the infested area for each year is shown above. Indications of weather characteristics are referred to criteria on p. 161. The years 1925, 1926 and 1927 were excellent to good years for chinch bugs, yet chinch bug populations did not increase. In 1928, which was an unfavorable weather year, the bugs increased with ultraviolet in the optimum range. In 1930, the weather was excellent but the ultraviolet too high and hence only a small increase resulted. In 1931 the weather was excellent, ultraviolet in optimum range, and there was a larger increase than in 1930; in 1932 good weather, ultraviolet too low, and only a slight increase; in 1933, unfavorable weather, ultraviolet in optimum range, good increase; in 1934, excellent weather with optimum ultraviolet and a very large increase; in 1935, optimum ultraviolet and very unfavorable weather and a sharp decrease; in 1936, excellent weather, ultraviolet very low, large decrease; in 1937 and 1938 ultraviolet optimum, weather unfavorable, slight decrease; in 1939 weather excellent, ultraviolet not recorded, slight decrease; in 1940 weather fair and variable from place to place, ultraviolet probably too high, a decrease of bug population. In 1941 ultraviolet was high, weather unfavorable, and there was a decline of population almost to a minimum.

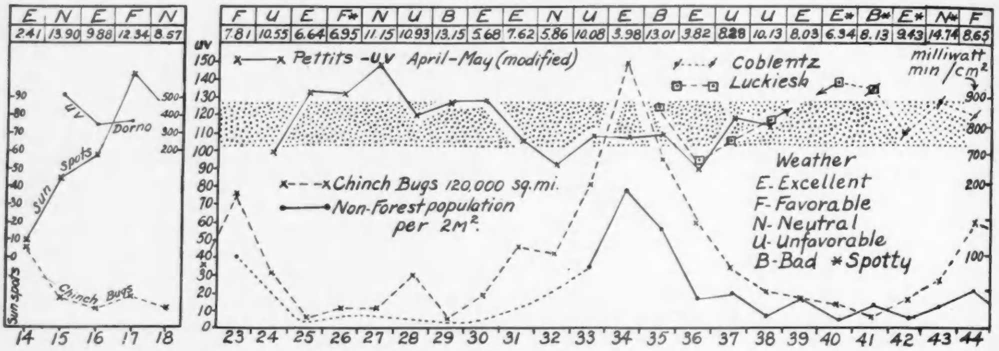

FIG. 9. The population of the chinch bug on 120,000 sq. mi. 1914-18 and 1923-44, scale of Shelford & Flint (1943) and the Trelease Woods non-forest population per 2 m², scale twice Fig. 4.

Ultraviolet light measurements: (a) Dorno, August, sun alt. 50°, 1915-17; (b) Pettit ratio, mean April-May (exceptions below), 1924-1938; (c) Luckiesh's figures E-v. equalized with Coblentz's figures reduced to mean monthly sums April and May, 1935-1941; (d) Coblentz, milliwatt min/cm², 1941 to 1944. Kendrick & Del Toro (1940) indicated that the daily summations for April and May in Puerto Rico averaged 9% higher in 1939 than in 1938. Such a value is roughly indicated by the dot in the base of the h, on the scale at the right. Absence of bug flight temperatures in April is adjusted by use of May data for 1926 and 1928 and 1/3 of April plus twice May data for 1944. The assumed optimum indicated by the stippled band is between Pettit's ratios 101 and 128 and between monthly means 737 and 887 milliwatt min/cm²; no definite relation exists between Pettit's ratios and milliwatts.

The weather is indicated by the figures for the May-June rainfall in inches and its character relative to chinch bugs, by a series of letters (E, F, etc.). The asterisk indicates spotty population; small changes in over-all population, attributable to local increases or decreases due to local weather.

Compare increases and decreases in populations with (a) the variation in the intensities of ultraviolet light with reference to the assumed optimum, (b) the May and June rainfall, and (c) the character of the weather. Note decreases and failures to increase (a) with too high ultraviolet intensity in 1925, 1926, 1940, 1941 and possibly 1927 (b) too low in 1936 and possibly 1932 (c) trends of total non-forest population, 1923 based on Weese (1924).

1942, 1943, 1944, and 1945, weather excellent to neutral, ultraviolet in optimum range, accompanied by population increases.

The period 1924-25 is brought to attention again because both years were characterized by a considerable increase in reproductive vigor, especially 1925 when there was flight and exposure of the insect to sunlight in late April. There was difficulty in finding an area with the insects abundant. The bugs used in the experiments were collected in Christian Co., Illinois, in the first few days of June. The adults and young were exposed to the sun in late April and all of May, which showed 74% of possible sunshine. Even with the great vigor shown by bugs from this population confined in experimental cages, they did not increase their range during 1925, but added slightly damaging populations in some surrounding counties in 1926 and 1927. In Christian Co. the damaging populations remained stationary in 1926 and 1927 though the weather conditions were almost perfect. This is a period in which the ultraviolet is assumed to have been too high. Pettit's readings were the highest of his period of study (Fig. 9).

The left portion of Figure 9 shows Dorno's record and that the chinch bug populations decreased when the ultraviolet was high and started to increase when it leveled off at a lower value, though the units of the scale cannot be harmonized with the other since there is no overlap for comparison of values.

Figure 10 summarizes the facts regarding ultraviolet light as a reproductive stimulus and the rainfall in May and June as a large factor in the mortality of survival of young chinch bugs. The April ultraviolet light is plotted with the May rainfall and the May ultraviolet with the June rainfall. It is only when both points fall within the limits drawn that the large populations occur.

The writer knows of no continuous or overlapping records of short wave solar radiation before 1924 or after 1944 except the short Dorno record.

1. History of Chinch Bug Population

A. General

The large 1944 population came just at the beginning of increase in sunspot numbers. The sunspot numbers increased very rapidly to an unusually high point. They were accompanied by an increase in May-June rainfall. Turning to the period previous to 1924, no solar records except the Dorno isolated ultraviolet for 1915-17 and the sunspot numbers are available. Reference to Shelford & Flint (1943, p. 451) indicates that no peak of chinch bug population has fallen in the year of a sunspot maximum. However, every sunspot decline period (lasting from 3 to 9 years) has been accompanied by a peak or a large increase in chinch bug population through and including 1944. If the yearly sunspot average is used, there is a total of twelve increases between 1823 and 1947. The 1848 to 1856 decline had two

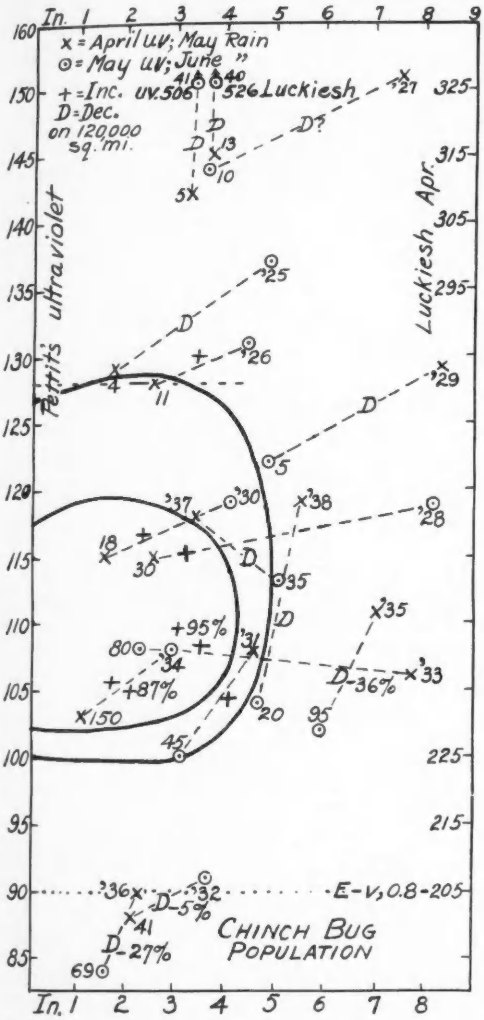

FIG. 10. A double ultraviolet hydrogram for the chinch bug on 120,000 sq. mi. The Pettit (I.A.U.) ultraviolet index for April is plotted with the rainfall for May (X); the May ultraviolet is plotted with June rainfall (O) because ultraviolet influences reproductive vigor of the chinch bug and rainfall is important in mortality of survival. The Pettit scale with decimal points omitted is shown on the left. The Luckiesh scale for April is shown on the right with center figures omitted because they do not follow the trends of the Pettit scale. This is due to the additive character of the Luckiesh data, to the effect of clouds and to city smoke. The May scale could not be used because the readings are much larger than those for April. Each pair of points (X and O) is connected by a broken line. The year is shown at the May-June (O) points. The size of population (Shelford & Flint 1943, scale) on the X April-May points, a D indicating decrease or a + indicating increase is placed adjacent to the connecting line. An oval is drawn around the largest increase and largest population (damage). Outside this another oval representing a less favorable combination of months is shown. All increases have one month within the ovals.

marked chinch bug population increases, the year 1852, with no damage, falling between the two peaks. There has also been a peak of population during each sunspot increase except in the 1833-1837 increase period. Figure 11 shows that the 1944 to 1947 increase in sunspots began from an April, 1944, average of 0.3 and increased regularly so that even this July peak of population fell in the period of sunspot increase. Large populations have carried over the sunspot minimum in four recent cases (Fig. 11). It must be emphasized again that the sunspots are not a fundamental phenomenon directly influencing organisms. Furthermore, they are not at all closely correlated with phenomena which are effective on the earth's surface and are in themselves subject to considerable irregularity.

B. HISTORY 1866-1947

Beginning in 1866, populations of chinch bugs are considered in Fig. 11 in relation to their most sensitive periods. These fall in April, May, June, and August. The sunspot curve is the mean number for April through May. Within any month there are marked variations in sunspots. In April, 1934, the daily records varied from 0 to 33, and in May, 1934, from 0 to 46. The number increased over several days followed by declines to 0 again. Stetson (1947) has pointed out that according to Clayton (1943) these high sunspot periods are preceded by high temperatures and followed by low temperatures and peculiar temperature fluctuations.

The chinch bug outbreaks previous to 1860 probably were not very well evaluated and the amount of land under cultivation was small during the period from 1823 to 1865 (Riley 1870, Forbes 1889a, 1889b, 1916; Howard 1888; Webster 1907). Starting with the conditions in 1866-1870 there was no reported damage in 1866. However, the population in the area of the 1871-1874 outbreak centering near Peoria may be assumed to have been present and increasing in 1868 and 1869. Using 9.5 inches as the statistical upper limit of favorable conditions, the reader can follow the rainfall in Figure 11, which is shown in tenths of inches on the three-purpose scale. The rainfall for the small areas of isolated outbreaks (cross-hatched) is shown by broken lines.

The 1868 (the first year of sunspot increase) small local population centering in southern Illinois south of the latitude of St. Louis (Fig. 11, S1) decreased to insignificance in 1869 with moderate rainfall and sunspots and probably high ultraviolet. The daily distribution of rainfall is not known.

A chinch bug outbreak that centered near Peoria, Illinois, and covered the northern three-fourths of the 120,000 square mile area, began in 1870 following excessive rain in 1869. Damage was severe in about the central half of the north-south extent of the area. There was a large chinch bug population in 1871 followed by a much smaller population in 1872 and a still larger one in 1873. The April and May sunspots from 1866 to 1870 fell to a low average of four in 1867 and rose to an unusual high of 176 in May, 1870. The large chinch bug increase came

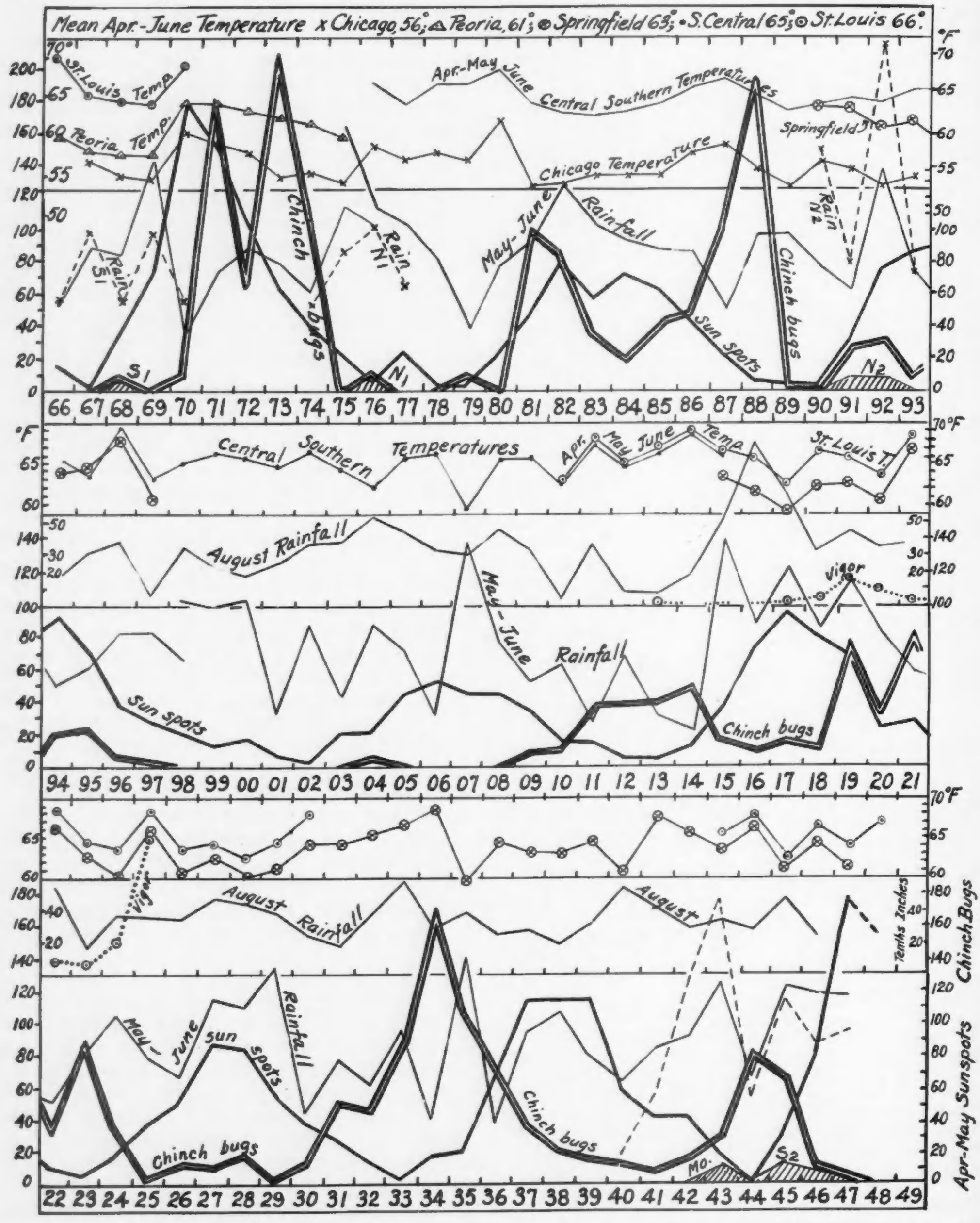

FIG. 11. Shows chinch bug populations, average April-May sunspots, and May-June rainfall in tenths of inches for infested areas on 120,000 square miles with Illinois as a center, from 1866 through 1948; all three are to be read on the main scale; chinch bug scale 1.33 times that of Figure 9. The small independent outbreaks—two in southern areas 1868 and 1943 to 1947, and two in northern areas, 1876 and 1891 to 1892—are cross-hatched but included in the total. They represent isolated infestations, at a distance from the main outbreak with individual histories; chinch bug vigor is illustrated for 1913 and from 1917 through 1925.

The temperature (°F) throughout the period is shown for the weather stations nearest to center of the infested area. Where there are fragmented areas several localities are shown for both temperature (°F) and rainfall (0.1 in.). August rainfall is shown from 1894 through 1946 on a separate scale. When two or more widely separated localities are involved, separate overlapping rainfall records are shown, e.g., 1875-77, three are indicated, the broken line for the northern Illinois independent outbreak; a solid line to the end of the 1870-75 outbreak centering in central Illinois; and another for the beginning and succeeding years of the 1879-1884 outbreak centering in southern Illinois (see maps in Shelford & Flint 1943). Higher temperatures and increased rainfall accompany the sunspot peaks but with notable exceptions, e.g., temperature 1937-1939, rainfall 1870-1871 (Mosier 1918).

in the following year (1871) which was the first year of the April-May sunspot decline probably accompanied by a decrease in ultraviolet. By 1875 the sunspot numbers had dropped to 20. The 1874 chinch bug decline, which brought the chinch bug population to almost half of that of 1873, could hardly have been caused by rainfall since the May-June rainfall average was only 6.02 inches (1874) for the infested area and temperatures were above average (Fig. 11). The daily distribution of rainfall is, however, not known in any cases before 1887 because records were not preserved. There was a small outbreak, N1, 1876 occurring in northern Illinois associated with a secondary low sunspot number. This (Fig. 11, N1) could possibly be interpreted as a fragment of the earlier large central Illinois outbreak. It affords no basis for special interpretation.

The 1881 through 1888 variations are in accord with probable usual relation of sunspots, ultraviolet and bug population (see Figs. 1 and 9).

In the case of the 1888 increase and the sharp decline of 1889 the rainfall was at the upper favorable limits in both years, 1888 (9.48 in.), only slightly lower than 1889 (9.83 in.). There are reports of fungus attacks in 1887 and 1888 (Swenk 1925), but no mention of such attacks in 1889 has been found. Figure 7 shows the climographs of 1888 and 1889 to be unusually similar. Analysis with ten-day climographs showed that at Morrisonville, Illinois, and Greenville, Illinois, 1889 was a better year for chinch bugs than 1888. Again we assume that short wave radiant energy was too high, because of ozone disintegration. The period 1897 to 1908 appears to have been one of solar irregularity and small sunspot numbers. It was almost without chinch bug damage though weather was favorable (see p. 165). It was a period of moderate solar activity (Clayton 1943, Vol. I, p. 48). The absence of the chinch bug in large populations must again be assumed to have been caused by variations in solar short wave radiation, probably in the direction of too little. There was a small increase in chinch bugs in 1909 preceded by only one favorable year. This was the beginning of the 1910-1915 chinch bug outbreak described by Forbes (1916). Declining in 1915 when short wave radiation was high (see Dorno, Fig. 9), the bugs remained at a low level until past the 1917 sunspot maximum for April and May. There was a large increase in 1919 during which the May-June rainfall average of more than 10 in. would ordinarily have been highly unfavorable. The preceding temperatures were at and below average, which is unusual.

The chinch bug, solar ultraviolet and weather have been rather fully discussed, 1924 through 1941. The relation of these phenomena to sunspots can be followed in Figure 11. A small outbreak (S2, 1943-1947) came in northeastern Missouri, 10 months before the sunspot minimum (April, 1944) with May-June rainfall of 17.44 in. (average of the 5 counties showing chinch bug increases). This population nearly faded out in 1944, increased in 1945 but disappeared by 1948. It continued one year after the end of the large outbreak and the sunspot maximum, which came in May, 1947 (Fig. 11). Further inspection of the large area of heavy population and comparison with monthly sunspot records shows that the 1923 peak of population came at the beginning of the sunspot increase. In 1944 the minimum came in April and the increase began in May. Previously, however, there have been no maximum populations which fell nearer than one year to the April-May sunspot maximum. This is in accord with the idea that the ultraviolet light usually increases during the sunspot increase up to a year or more before the maximum (Fig. 1) when radiation exceeds the limit of toleration of many organisms. After this it is reduced through the development of ozone.

2. The Causes of Population Spottiness

The question naturally arises as to why chinch bug populations are spotty. The general outlook is changed when upper statistical limits of May and June rainfall usually tolerated is raised from 5.5 to 6.0 in. Rainfall relations were analyzed by Shelford & Flint (1943) and Thornthwait (1936) was quoted. The cases used and figures presented are correct and valid but solar radiation must be considered. The cases cited herein include several in which weather could not reasonably have been the cause of the increase or decrease or failure to increase or decrease. There are many factors which can lead to spottiness due to short wave radiation. There are ultraviolet flares about which there is very little information. The ultraviolet intensity varies from day to day. In April, 1934, Pettit's (1932) readings varied from 0.88 to 1.22 and in May from 0.96 to 1.20 (decimal points are omitted elsewhere). The insects in different areas will come out of hibernation at different times, those farthest south earliest in the season. The insects will probably be in flight only on sunny days, but these will be different days in different areas.

The region occupied from time to time by large populations of chinch bugs is a parkland. Areas of tall grass prairie are interspersed with groves and stream-skirting deciduous forest. The autumnal flight of adult chinch bugs takes them into these forest areas in some abundance for about 100 ft. (30 m) and scatters some throughout the small forested areas.

In the spring some chinch bugs will be at the south edge outside a woodland, others at varying distances inside the woods. The date at which they leave hibernation quarters in spring has been shown to vary directly with the distance into the woods at which they were located at the beginning of spring. In the experience of the writer the departure from the hibernation quarters may extend over three weeks. In localities without woodland, most of them probably take flight at more nearly the same time, which lessens the chance of differences in the amount of ultraviolet received. The chances of spottiness

in vigor occurring due to the direct effect of radiation are greater than if due to indirect effects of radiation on food.

3. Geographical Relations

One very important geographic connection with this paper is a report by Dahms & Osborne (1942) on chinch bug abundance near Lawton, Oklahoma, from 1916 to 1940. The annual rainfall at Lawton is 8-10 inches less than at Champaign-Urbana, and these authors came to the conclusion that the period from July 10 to August 20 was very important. When this rainfall was low, infestations were light the following year. This is because the population which is to overwinter is reduced to a very low level, due to exposure of eggs and young to drought so that they cannot build up to a heavy damaging level in one year. It is furthermore difficult to compare a single locality in Oklahoma with 120,000 square miles elsewhere because of minor shifts in populations in relatively local areas. However, the increase appears to be two to three years earlier than in Illinois; population changes at Lawton in 1916, 1917, and 1918 appear to correspond to those of 1919, 1920, and 1921 in Illinois; Lawton, 1920, 1921, and 1922, to Illinois 1922, 1923, and 1924, etc. A sharp decline came in Lawton in 1935 and in Illinois in 1937. The average hours of sunshine is a little greater in Lawton than in Illinois and much greater in the critical months of July in Lawton than in the critical April or May in Illinois. Forbes pointed out that the 1910-1914 Illinois outbreak began two years earlier in Kansas and Nebraska. If ultraviolet light is as important as the correlations indicate, as it increases over several years, the western areas with less April and May cloudiness would probably receive optimum exposure at lower intensities than the more easterly areas.

4. Discussion of the Chinch Bug Relations

Because of the variation in vigor of bugs and the marked effect of ultraviolet light on organisms, the account has been written from that viewpoint but, at the same time, it is recognized that the results may accrue through the food supply. Furthermore, the electric phenomena associated with solar phenomena are not forgotten. While Stetson (1947) has discussed the electricity, he showed no record. Sabrosky, Larson, & Nabours (1933) used Cooper-Hewitt Mercury Lamps in plain glass the first year and in a Corex D tube in the 2nd year studies. The spectrum of both types of tubes is high in short wave violet. White light was supplied by Sylvania clear bulbs. This light was supplementary to the regular varying winter greenhouse light. The insects were the grouse locust, *Acrydium arenosum angustum* Han. The relative fertility was 42.8 per cent under "white" light, 54.05 per cent under "violet" light, and 0.0 per cent among the controls. The average period from date of mating to the appearance of young was 60.6 days for those under the "white" light and 55.0 days for those under the "violet." A mortality of 41.8 per cent was recorded among the 141 under "white" light, 30.9 per cent in the 126 under "violet" light, and 72.1 per cent among the 122 controls, showing a highly significant greater survival of the offspring kept under the lights. These experiments show that short wave length radiation may increase fecundity.

Dahms et al. (1936) pointed out differences in fecundity and length of life of chinch bugs feeding on two different varieties of sorghum and cited other studies in that field. Influence of food supply on the reproductive capacity of the chinch bug has been demonstrated. Dahms (1947), and Dahms et al. (1936 and 1940) cultured chinch bugs on sorghum grown in nutrient solution. Females grown on plants in culture media produced most eggs when phosphorus was low and nitrogen high. The length of life of the females on such plants was only very slightly increased. Egg production also varied with the variety of plant. Evidently the mineral content of the culture medium influenced the egg producing capacity of the females. The results, however, do not indicate the kind of vigor and prolonged reproduction which characterize vigorous bugs. The general facts relative to light and its bearing on populations coupled with the importance of weather, make the studies of Dahms (1947) have greater meaning.

One peculiar thing about the 1925 high vigor in experimental climate-simulating cages was the fact that the vigor continued beyond the generation exposed to light and fed on out-of-door plants. The insects used were first new generation nymphs (called second generation) in the third and fourth instars. They were captured early in June because earlier there was difficulty in finding a place where chinch bugs were abundant enough to capture in considerable numbers. In the laboratory all the second, third, and fourth generation nymphs were behind three to five thicknesses of double strength window glass (Shelford 1932; Shelford & Flint 1943).

VII. FOREST-EDGE VERTEBRATES

The chief forest-edge vertebrates at Trelease Woods which are year-round residents are the cardinal, song sparrow, bob-white, and cottontail rabbit. Of these we have the best local data on the cardinal and the best state-wide data on the cottontail; in other localities we have good bob-white population records. The record of the cardinal is interrupted by several gaps (Kendeigh 1944), but the existing data fall into a possible ultraviolet-hydrogram. The song sparrow records are missing.

The bob-white or quail, *Colinus virginianus* (Lin.) has only one brood annually, but there are often a few renestings when nests have been destroyed. It has been noted as present during the winter bird censuses and in the spring, but there have been few censuses of breeding pairs in the edge of Trelease Woods or of populations in the vicinity. The nearest study was made by Yeatter (1943) at Hunt City, 75 miles south and a little east of Trelease Woods. The Yeatter data will be discussed later in connec-

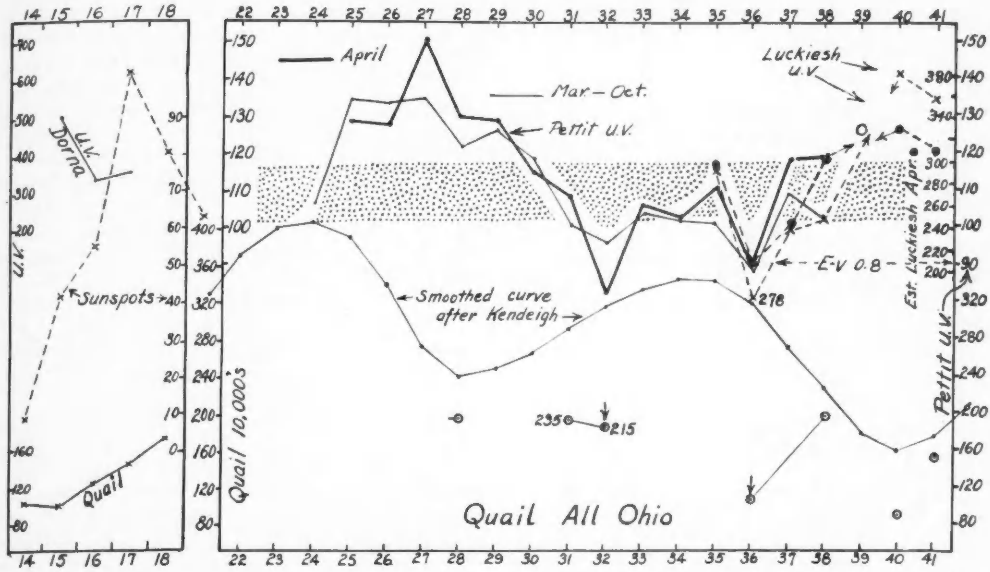

FIG. 12. The population of quail in Ohio is shown as Kendeigh's 1944 smoothed curve with the counts in the absence of snow indicated by circles; following the general plan of Fig. 9, which see. The scale is in tens of thousands of birds in the entire state. Both the April and March-October ultraviolet are shown (1924-41), but the April condition is most important. Estimated Luckiesh figures are shown for 1940 and 1941. The Dorno data duplicate those of Fig. 9. When the actual "no snow" counts are considered along with the smoothed curve decreases, correlated with too little or too much ultraviolet, may be noted in connection with April ultraviolet for 1925-28, 1931-32, 1932-36, 1938-39, and 1940. In 1941 doubtful estimate from Luckiesh's data is not in full accord. Kendrick & Del Toro (1940) reported April noon maxima for 1939 about 12% higher than 1938 in Puerto Rico. The open circle is the rough location of such a value on the scale at the right.

tion with other localities having longer records. The work of Errington (1945) provided a good series of records for Wisconsin and Iowa. The longest record is shown in a graph compiled by Kendeigh (1944).

Kendeigh's 1944 graph covered the quail population of Ohio based on the Christmas bird censuses from 1908 to 1941 (Fig. 12). This curve, like that of the chinch bug, makes possible examinations of the relations to available ultraviolet light. Fig. 12 emphasizes all the relations brought out by the corresponding chinch bug graph, Fig. 9. The suggested ultraviolet optimum is about the same (102-117). The Pettit data for April are shown with April-October and with the records of Dorno (1919) and Luckiesh (1946). It was necessary for Kendeigh to draw a smoothed curve taking into account the effect of snow on the counts of quail. His curve assumes the snow counts were high and the non-snow counts low. Only the data obtained when there was no snow on the ground are indicated on Fig. 12. It is noteworthy that the non-snow count in 1932 decreased as compared with 1931 when the ultraviolet fell below the suggested optimum and that again in 1936 the non-snow count was very low with ultraviolet very low. Furthermore, the non-snow count in 1938 was high with ultraviolet at optimum and very low again when it was above optimum.

The Ohio quail data were also plotted (Fig. 13) much as in the case of the chinch bug (Fig. 10) for the month of April. The ultraviolet and rainfall data for the quail in April were plotted as X's and the mean rainfall and ultraviolet data, March to October, were plotted as circles (1925-38). The two items are connected. The percent increases or decreases as compared with those of the preceding year are indicated. In the case of the increases both items fall within the ellipse and lie between 2 in. and 4.5 in. of rain and 98 and 116 on the ultraviolet scale. There are no increases outside the limits drawn and no decreases with both items within the ellipse. The 1931 May through October ultraviolet fell below the lower limits of optimum but April is most important.

The relation to sunlight was studied. The Ohio sunshine record from the Weather Bureau is the average for the entire state. It includes four stations well placed in Ohio and, in addition, Fort Wayne, Indiana, Pittsburgh, Pennsylvania, and Parkersburg, West Virginia. The population of 35 years when plotted on April percent sunshine and rainfall shows that increases in population over the preceding year fall mainly between 1.5 to 2 inches of April rain and between 41% and 64% April sunshine on the low rainfall side. On the high rainfall side they lie between 65% and 55% at 4.5 in. Most of the decreases lie below 56% sunshine with more than 3 in. of rain. There were three decreases with sunshine above 63% and rainfall ranging between 1.4 and 3.1 in.

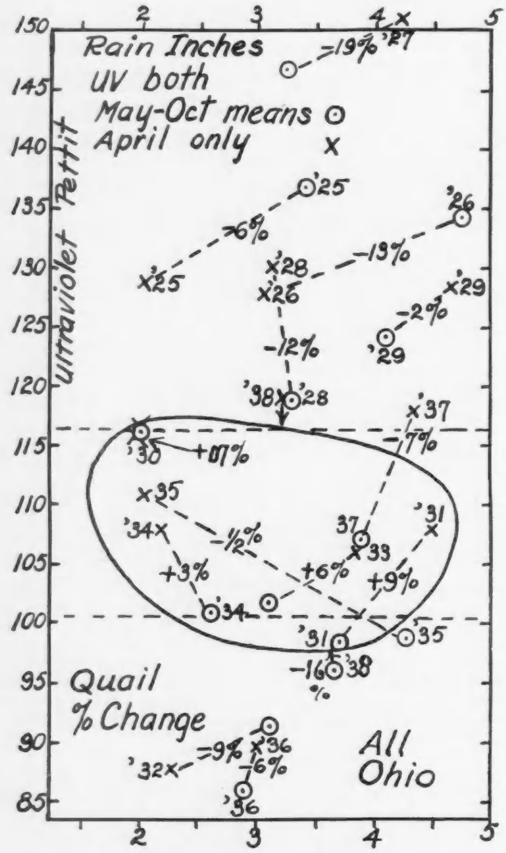

FIG. 13. A double ultraviolet hydrogram for quail population in Ohio 1925 through 1938; follows the general plan of Fig. 10, which see. Changes in population are indicated by percentage increase (+) or decrease (—). All increases fall within the ellipse and all Aprils with increases fall between 101 and 116 limits on the Pettit scale. April rainfall for all Ohio and April ultraviolet are used for the reproductive stimulus period and monthly mean May to October data are used for the developmental period of the birds.

There have been excellent quail studies near Madison, Wisconsin, and in Iowa. Errington (1945) has summarized most of the studies in detail. Quail-nesting operations begin in April in southern Wisconsin (Prairie du Sac and Lake Mills). The counts were made in November and represent summer increase and the weather and radiation data were studied for April and the period April through October. Rainfall, number of rainy days in the area, and the relative humidity were utilized in the studies of relations to autumn population and percent of increase in population.

The rainfall at Prairie du Sac showed the usual variations from that at surrounding stations. To overcome the characteristic spottiness, the Prairie du Sac monthly rainfall was averaged with that at four surrounding stations: Hillsboro, Richland Center, Portage, and Madison. There are obvious difficulties regarding percent of sunshine not recorded at Prairie du Sac. The La Crosse figures are nearly always higher than those of Madison, frequently 10% or more, which is relatively cloudy in the open season. La Crosse is approximately 80 miles northwest of Prairie du Sac and Madison 24 miles southeast and out of line of prevailing winds. Dubuque readings are usually a little higher than those of Madison. None of the places mentioned represents Prairie du Sac, but Madison was used because of nearness. The same criticism applies to humidity as to percent of sunshine. The faulty records did not make a good diagram. The records should be at the point of observation of populations. This is especially true of sunshine, ultraviolet, and relative humidity.

Pettit's ultraviolet index has not been modified for cloudiness. It represents the general world condition of ultraviolet intensity which is modified in different localities by atmospheric conditions, etc. Sunshine recorders are adjusted to record the sunshine when the shadows are barely visible, and since there are few overcast days in the period April through October, the off-and-on effect of moving clouds on ultraviolet are unpredictable, and in fact most animals control their exposure to sunlight. The Luckiesh readings by months were read from figures for 1935 through 1938 in Luckiesh, Taylor & Kerr (1939, p. 427) and from photographic prints supplied by Dr. Luckiesh. He published only the totals for 1940 and 1941 in erythermal units which are approximately 1.5 times his E-viton unit (Luckiesh 1946) to which they were converted. No figures were published for 1939 but are reported to be proportional to those of the preceding and following years. The monthly values were estimated for 1940 and 1941 from the average proportion of the total which each month represented in 1935-38. His low winter readings are least applicable because of greater cloudiness in most localities and because of city smoke. His April-October records are good indications of ultraviolet intensity in other localities. The means between the figures for 1938 and 1940 are used for 1939 where necessary, but not much dependence can be placed on figures for single months in 1940 and 1941 and less on the 1939 estimates. The increases and decreases of the Pettit and Luckiesh figures are in general agreement 1935 through 1938.

Figure 14A shows an ultraviolet-hydrogram of the quail population at Prairie du Sac. These and other quail populations are from Errington (1945). April ultraviolet is used with April-October rainfall. Figure 14B shows ultraviolet-hydrogram for the percent increase in population, using the April-October data on ultraviolet of both Pettit and Luckiesh. There are four overlapping points and the data for 1940 and 1941 none of which are not discordant. For the corresponding ultraviolet-hydrogram in which only April data are used see Figure 19B (p. 176). Figure 14C shows the population data plotted on the April-Octo-

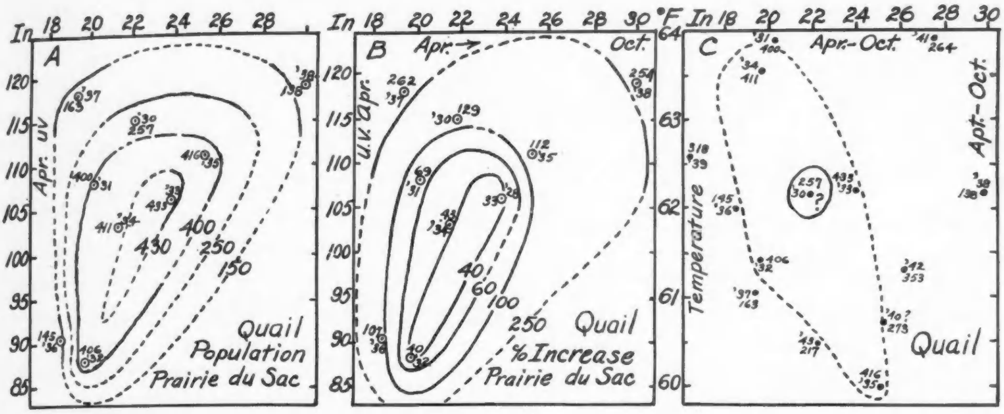

FIG. 14. The relations of quail, November populations and percent increase at Prairie du Sac, Wisconsin, 1930-1938, to ultraviolet light using Pettit's indices to rainfall and to temperature; all population increase figures are available in Errington's (1945) paper.

A—An ultraviolet-hydrogram of autumn quail population 1930 to 1938. The rainfall is the average of that of five weather stations near and surrounding the study area, April through October. The ultraviolet is for April alone; the figures are population size.

B—An ultraviolet-hydrogram same as A but the figures are percent of increase in quail population during the late spring, summer and early autumn. Compare with A and note shifting 1930 and 1935 populations from different categories to the same category, etc. For a similar diagram using only April data see Figure 19B.

C—Indicates the impracticability of drawing a thermo-hydrogram for this autumn quail population. Note population 257, 1930 in the center of the 400 population line and 115, 1936 nearer the 400 line than 318, 1939.

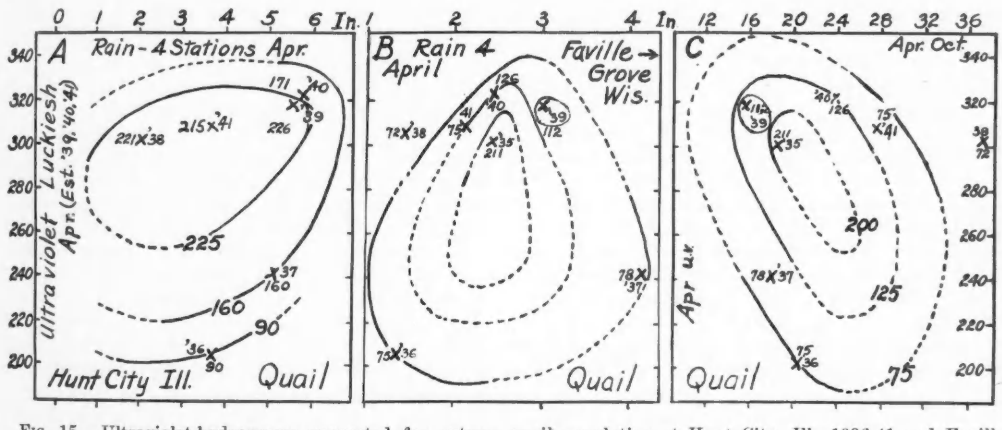

FIG. 15. Ultraviolet-hydrograms suggested for autumn quail population at Hunt City, Ill., 1936-41 and Faville Grove (Lake Mills), Wis., 1935-41, using only Luckiesh's data and estimates therefrom in E-viton hours.

A—Hunt City poulation ultraviolet-hydrogram using April data only; for similar diagram for Prairie du Sac population, see Fig. 19B, p. 176. Both suggest population control by April conditions.

B—Same as A using Faville Grove population.

C—Faville Grove population using April-October rainfall with April ultraviolet. Rainfall is the average of 3 or more surrounding stations, to eliminate spottiness.

ber rainfall and temperature. Obviously no thermo-hydrogram can be drawn. Figure 15 shows the ultraviolet-hydrograms of the Hunt City, Illinois (Yeatter 1943), and the Faville Grove, Wisconsin, populations (Hawkins 1940). The ultraviolet-hydrograms are drawn with reference to the Priarie du Sac data, which are more nearly complete. Figures 14 and 15 show the use of April ultraviolet with April-October rainfall, and both sets of data for April only. April-October rainfall are used in Fig. 15C and the form of the hydrogram is somewhat different but the general principle is the same. These comparisons indicate that the April conditions are most important in controlling population.

The Ames, Des Moines, and south central Iowa data are plotted with similar ultraviolet-hydrograms in Figure 16. There are only three items for south central Iowa for the years 1936, 1937 and 1938 (Fig. 16B). They, however, were in the same order of magnitude and varied in the same direction from year

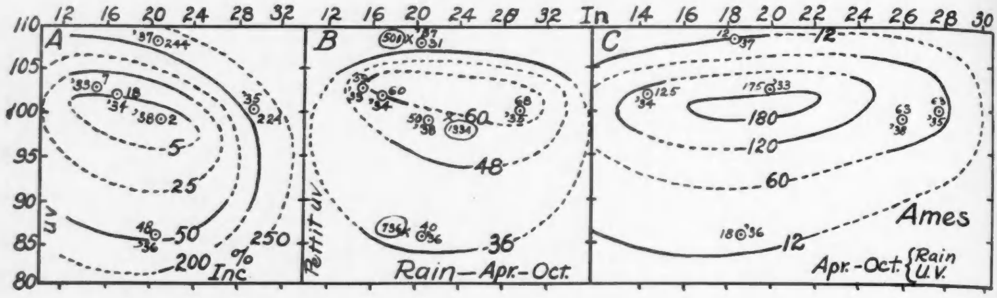

FIG. 16. Ultraviolet-hydrograms of Iowa autumn quail population using Pettit's April-October ultraviolet data and April-October rain at the nearest weather station, 1933-38.
A—Percent increase in population at Des Moines.
B—Population size at Des Moines. The southern Iowa data are included and encircled. Note that 736 corresponds to 40 at Des Moines; 1334 to 50; and 501 to 31—same general relations being indicated (Sanders 1943).
C—The Ames quail population drawn on the same ultraviolet data as A and B but with the scale for April-October rainfall double to agree with that used for Prairie du Sac, Fig. 14. Note the elongation of the ultraviolet-hydrogram which would otherwise be similar to that in B.

to year as the Des Moines population. There were some sharp differences between the rainfall and populations at Ames and Des Moines, but the April-October diagrams are similar. In central Iowa where rainfall is more variable the ellipses fall into a nearly horizontal position when plotted on the same scale as for Wisconsin[1] localities. When the rainfall scale is reduced to half, as shown in Figure 16B, the general form is changed, the scale of Figures 14A, 14B, and 16C are the same.

A number of the figures show total autumn population of quail falling into an orderly pattern with reference to two factors regardless of the size of the parent population within the limits of the available data. For example in an extreme case at Prairie du Sac, Wisconsin, a spring population of 288 was followed by an autumn population of 411 while a spring population of 196 was followed by an autumn population of 416 (Fig. 14A). However, the first represented an increase of 43% and the second of 112%, and both fall in an ultraviolet-hydrogram shown in Figure 14B. The fact that populations can be plotted on comparable figures results from the fact that (a) the percent of increase is roughly inversely proportional to size of the parent population; (b) the summer mortality is quite uniform from year to year in the years which have been diagrammed; and (c) the ultraviolet and violet light, one or both, are evidently a reproductive stimulus especially in combination with moisture, and evidently increase the vigor of the young and thus help to build populations toward a habitat saturation and thus make up for deficiencies in parent stock. (See Nestler, DeWitt, & Derby 1949.)

In the case of the quail, combinations of humidity and ultraviolet light usually give symmetrical results just the same as rainfall. A number of rainy days gives less successful results but results not wholly inconsistent. In some of the cases percent of possible sunshine and a moisture index give results approaching parallel ellipses. The percentage sunshine humidity diagrams were good in the case of prairie chicken at Hunt City, Illinois (Yeatter 1943), are not wholly inconsistent for butterfat in cows' milk for all of Illinois (Shelford 1950).

It proved impossible to draw parallel ellipse temperature-moisture diagrams (thermohygrograms or thermohydrograms) with the Wisconsin and Ohio quail population data. They were as fully contradictory as in the case of chinch bugs (Fig. 19A). Combinations of sunshine and ultraviolet light with temperature also give contradictory results in a large number of cases tested.

The cottontail, *Sylvilagus floridanus mearnsi* (Allen), according to Koestner's Trelease Woods trapping records, was most abundant in 1939 and only slightly less in 1938 (see Koestner 1939). R. E. Yeatter of the Illinois State Natural History Survey and David H. Thompson of the Forest Preserve District of Cook County, Illinois, have worked over the available Illinois population records since 1925. From 1925 through 1929 estimates are based largely on the central Illinois records of Joe L. Mote (Yeatter & Thompson 1951). The Yeatter & Thompson estimates are from 1925 through 1949 and cover available ultraviolet light records. The writers point out that in many years population levels vary considerably in different parts of the state. Their population estimates are much less reliable than Kendeigh's Ohio quail curve, since they are not based on counts in a representative number of localities on the same date. The population estimates are made of impressions of a number of field men, hunting records, local censuses, automobile kill, etc. According to Yeatter (personal communication) rabbits breed in three periods, March to mid-May, mid-May to late July, and August-September or a little

[1] The slope of the rainfall-sunshine diagrams is usually from left at the top to right at the bottom. There is a tendency toward more sunshine when rainfall is low. Under the same conditions the ultraviolet diagrams usually slope from right at the top to left at the bottom. Evidently ultraviolet light tends to be high when rainfall is high east of the Mississippi River. Much of the general form of the graphs is determined by scales.

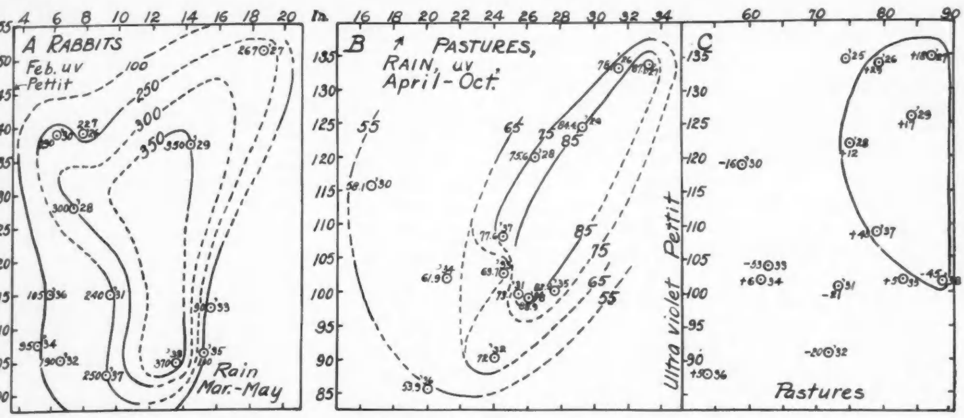

FIG. 17. The climatic and food relations of cottontail rabbits in all of Illinois.
A—An ultraviolet-hydrogram using February ultraviolet as affecting reproduction and March, April, and May rainfall sum as affecting survival of young rabbits. The very low percent of possible sunshine may have adversely affected the ultraviolet intensity in 1926, 1928, 1935, but the rabbits themselves probably control the exposure to sunlight to a large extent. The diagram is irregular but no discordant.
B—An ultraviolet-hydrogram of Illinois pasture conditions as indicating rabbit food supply and shelter. Irregular values are for 1931 and 1933 when the forage plants, according to crop reports, were damaged by adverse winter conditions (see Climatological Data). 100 indicates excellent pasture; April 1945 was rated 101, July 1945, 99, and July 1934, 25, in dist. #1 of the state.
C—The relation of population increases above 6 percent to pasture conditions and ultraviolet light, April-October. The half oval encloses increases of 12 to 45 percent (1938 = + 45% not — 45%).

later. The first breeding period is usually most important as regards its influence on the population. The ratio of relative importance in the seasonal order is regarded by Yeatter (personal communication) as being 3, 2, 1 (see also Schwartz 1942). In addition, the rabbits are subject to death from tularemia and probably from other pathological conditions (Ecke 1948). Tularemia is least prevalent in the first breeding period. The complications present a problem as regards which condition, of rainfall, of sunlight, of ultraviolet, or of other factors had greatest effect on the population.

It is obvious from the examination of the cottontail population data that no general relationship such as is shown in Figures 9 and 12 can be demonstrated. The assigning of a value of 3, 2, 1 to the respective generations does not clarify the matter. Ecke (1948) states that mature sperm began to appear in the seminiferous tubules as early as mid-January but there was no large accumulation until late in February. He put the date of beginning of mating in central Illinois at mid-February. The assumption which we have followed is that light is important shortly before the mating period. Accordingly February ultraviolet was used wtih the March, April, May rainfall or relative humidity and gives the results shown in Fig. 17A. When the mean of January and February ultraviolet were used the diagram was less symmetrical.

Thompson (1941) analyzed the Illinois rabbit populations from 1929 to 1941. This study along with the others that have been consulted indicate that the population fluctuation in rabbits is unusually complicated. He used "scarce," "moderately abundant," and "extremely abundant" as categories, and temperature and rainfall climographs and monthly limits enclosures similar to those of Figure 6. The number of years is small and the diagrams do not show striking differences, but Thompson concluded that January and February were critical months for rabbits. Likewise, Shanks (1946) who made a similar study of populations of foxes, raccoons, and opossums in Illinois concluded that January through April made up the critical period for the populations of these animals.

Some clear diagrams, however, may be presented, viz., percent increase and decrease in rabbit populations in Illinois in relation to pasture condition. The Illinois Co-Operative Crop Reporting service compiles estimates of pasture conditions April through October of each year. The records 1925 through 1948 were made available to the writer through the courtesy of J. A. Ewing. Figure 17B shows the relation of these estimates to rainfall, April through October 1926-1948 and Pettit's ultraviolet light indices. The pasture conditions form an ultraviolet-hydrogram satisfactory except for 1933 and 1931. Both the preceding winters, especially 1933, are mentioned in Climatological Data as bad for grasses and cereals. Plants are weakened by certain types of winter weather conditions such as occurred in these years. Rabbits are dependent upon forage plants both for food and shelter. When the rabbit populations are plotted with ultraviolet light and pasture conditions as shown in Fig. 17C, the increases of population of 12% and above occur under pasture conditions of Crop Reporting Service—index 75-90 and ultraviolet light of 100 to 135 enclosed with a

half oval. No increase outside the limits exceed 6%. Six percent increases are not significant when the data are of somewhat uncertain character.

In the diagram (Fig. 17A), February ultraviolet represents reproductive stimulus and March through May rainfall possible mortality of young, food, and shelter for the young and for lactating females. These conditions may reasonably control the population in the largest litter, estimated as three times as important as the late summer litter—and much more important than the June-July litter. Accordingly conditions in these four months may control the population except for abnormally severe conditions between May and November, the month of censusing. Figure 17A shows that this diagram is rough but satisfactory as a series of ellipses. According to Yeatter, tularemia increases in the late spring and there is a possibility that the average losses of the first litter (March to mid-May) are merely replaced by the later breeding.

In comparing the Illinois population estimates with those of Wisconsin, it is noteworthy that one Illinois maximum came in 1929 and was followed by a Wisconsin maximum in 1932 (Grange 1949, p. 91). The second maximum came in Illinois in 1939 and in Wisconsin in 1942. In both cases the weather and population data are for the entire state. An examination of the two states on the basis of Hopkins' (1918) bioclimatic law makes it evident that in the advance of spring seasonal biological events, Illinois averages 30 days earlier than Wisconsin. Accordingly, the use of the March ultraviolet light with the April-May-June rain for Wisconsin rabbits gave a figure less nearly complete but closely similar to that of Figure 17A. Above a line that may be drawn from 110 on Figure 17A to 120 on Figure 17B (left sides of each) the Wisconsin diagram is very closely similar to that for Illinois. The Wisconsin data cover six fewer years than those of Illinois. The March ultraviolet is a greater factor of difference than the rainfall. In these years (1931-38) at least, March ultraviolet does not follow the trends of the February ultraviolet but appears to change quite independently.

Rabbit increases and decreases tend to fall into a widely restricted pattern when diagrammed with rainfall and percent of sunshine. More in the way of reasonable results was accomplished by the analysis than might have been expected in the case of a mammal usually with three litters, but varying from two to a possible four. This is especially significant when the fact that the other hazards of the rabbits are accompanied by a serious disease, hunting, and heavy predation. Tularemia has been found to be an important cause of rabbit declines at least locally. Yeatter & Thompson (1951) have pointed out that the maximum number of cases of tularemia in humans was reached during the fall and winter of 1938-39 before the maximum rabbit population of 1939.

VIII. LABORATORY STUDIES OF THE EFFECTS OF RADIATION AND ELECTRICAL PHENOMENA

During the period beginning in the early '20's, a large number of workers turned their attention to the effect of ultraviolet light on organisms. Usually such operators were interested either in medical physiology or in some commercial application. Commercial sources of ultraviolet light were used and a rather high intensity was applied for short periods. A method of this kind usually does not yield results of ecological application. The experimental results are sufficient to indicate that solar radiation and ultraviolet light may affect the physical well-being of adult organisms or their reproductive capacity (1) directly or (2) indirectly through their effect on the vitamin content or other characteristics of food plants.

The effects on plants are numerous and space permits the citation of only a few examples in accord with which there may be indirect effect on animals. Coward (1927) found that quartz mercury vapor light accelerated formation of Vitamin A in living plants. Heller (1928) found that seeds germinated in sunlight contained more Vitamin A than seeds grown in darkness, while Vitamin C was increased slightly and Vitamin B had not changed. Tojkin (1931) found that ultraviolet rays increased the amount of Vitamin D in certain plants. Arthur & Hawill (1934) found that certain exposures to mercury vapor lamp improved flowering of a number of well-known plants. Benedict (1934) found that wave lengths of 290 to 310 mμ increased dry weight and calcium content in plants, but had little effect on phosphorus. Etinge (1928) found that radiations above 289 mμ produce larger plants. Luckiesh (1946) showed certain largely detrimental effects of ultraviolet on plants. Shirley (1935) stated that wave lengths not in sunlight are usually detrimental to plants. Withrow & Withrow (1947) showed the effect of different wave lengths on several plants. They stated that no entirely satisfactory artificial sources of radiant energy for plant growth are available.

Figure 17B shows the relations of pasture plants, chiefly grasses, some clovers, and a few other herbs to ultraviolet light (1926 to 1938).

As to animals, Bissonnette (1938) summarized the work on the relations of game animals to light conditions. As to the older work, Davenport (1908, p. 426) quoted various authors to show that tadpoles, sea trout, pond snails, and young cats grow faster or larger in the same length of time in the light than in the dark. As to wave lengths, he quoted (p. 432) Beclard (1858) that flesh fly larvae were largest when grown under violet and blue light and smallest under green light. He tabulated (p. 435) Yung's (1878) results showing that tadpoles grew fastest and that eggs of squid, sea trout, and pond snails hatched quickest when subjected to violet light. However, Roney (1943) stated that Rugh re-

peated Yung's experiments with precision as to energy and found none of the differences described by Yung. The same may be true of much of the older work, but, while precise methods must be used, energy may not be the factor. There are physiological effects of specific wave lengths and the threshold of effective stimulation becomes of first importance. Roney using a species of the snail, Heliosoma, found effects in oxygen consumption and temperature relations under colored screens. Bartholomew (1949) found light intensity was important in the reproduction of the English sparrow in a study also devoted to the length of day.

As to effect of radiant energy on fecundity, there is considerable recent work of value. The number of ovulations in European domestic rabbits subjected to strong light by Smelser, Walton & Whetham (1934) was only slightly greater than in the animals kept in darkness. Haldane (1929) reports no results from exposure of fattening cattle from behind to mercury vapor lamps for short periods; cephalic exposure is probably essential (Benoit 1935; Benoit & Ott 1938). Stetson (1947) states (p. 182) that a pair of monkeys was induced to breed by careful application of ultraviolet light. Ultraviolet increases egg production in poultry (Bailey 1950). Sabrosky, Larson & Nabours (1933) and Marshall & Bowden (1934) did some ecologically significant short wave experiments discussed on page 177.

Luckiesh & Holladay (1933) wrote on units and terms for biological effects. Their suggestions have been followed. The E-viton unit is usable. The germicidal range has been established but beyond this there has been very little physiological classification of wave lengths.

It has not developed in this study that the length of day is an important factor in determining the size of populations, but no studies have been conducted in this field. However, light intensity and short-wave radiation in combination with moisture have been demonstrated to be important. Ultraviolet light appears to be of especial importance. The results appear to be good in spite of the absence of the on-the-spot records of the factors and conditions employed in the diagrams.

Electrical phenomena, especially differences in potential, have been studied by Burr (Stetson 1947). He suggested that the differences noted were correlated with certain phases of the moon. The moon is known to influence electrical conditions on the earth. These electrical potential studies have not as yet yielded any leads into further advances. Accordingly we must rule out any suggestion of electrical effect on organisms.

IX. OPTIMA, PAIRED FACTORS, AND THE USE OF STATISTICS

Most organisms show a point of maximum functioning and of an optimum condition for existence with respect to normal weather and physical factors. In the case of the quail, the large autumn populations have fallen between 18 and 27 in. of April-October rain and between 2.0 and 3.5 in. of April rain. There can be too much as well as too little rain. It is known in the case of chinch bugs that a moderate amount of rainfall in April and early May is favorable to a large population (Shelford 1932, p. 539). There is no evidence to show whether or not there is a direct effect on the bug at this point, but rainfall is very important later within limits noted on p. 177.

Maximum functioning with respect to moisture is indicated in the hygrothermogram of the codling moth pupa (Fig. 18A). This principle is evident in the various diagrams presented in Figs. 18B and 19A and B. Even though the involved organs and their functions are not known, these diagrams indicate the rate of function and the limits of favorable and unfavorable conditions. There appears to be no definite agreement as to the relations of function and organs in cases where light has been shown to modify animal functions (see Clark 1922). Only a little is known in this respect in the case of terrestrial animals, especially invertebrates, in their relations to temperature and humidity in combination even in cases where thermohygrograms have been drawn. It is, however, supposed that there is an effect of the two factors in combination which does not occur in the same way when they operate separately.

Regarding the relation of maxima or optima for plants in relation to light, Shirley (1929) states that at low light intensities the dry weight produced by

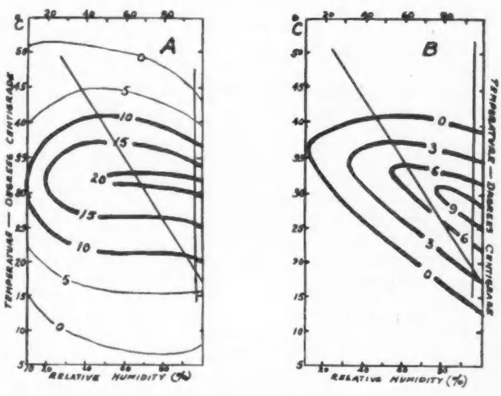

FIG. 18. Thermohygrograms for the rate of development of the codling moth pupa and the first instar of the chinch bug.

A—For the codling moth pupa only the part of the diagram in heavy lines was used to show a correlation of rate with temperature of 0.10 and of rate with humidity of 0.32. The whole chart showed a correlation of rate with humidity of 0.03 and with temperature of 0.73. The vertical line on relative humidity 95 which would be the condition on cloudy, rainy days would be contrasted with the oblique line which is the condition on sunny days, and it is readily seen that the correlation would be quite different.

B—For the first instar of the chinch bug which showed a correlation with temperature of 0.25 and with humidity of 0.63. The vertical and oblique lines again indicate the difference in correlation which would occur on cloudy rainy and on sunny days.

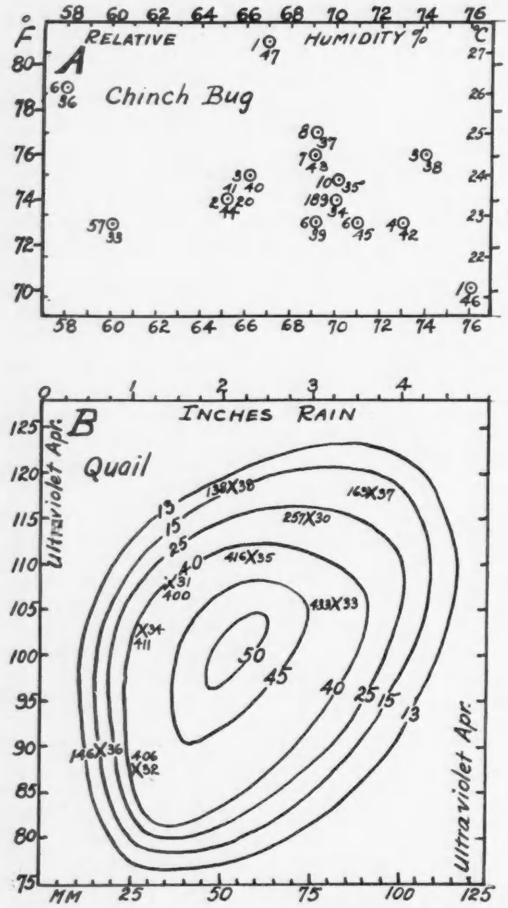

FIG. 19. The correlation of chinch bug and quail populations with conditions.

A—The distribution of chinch bug populations as shown by autumn-winter collections, when plotted on the temperature and humidity chart. The correlation of population with temperature was 0.40 and with humidity 0.00. With no correlation with humidity, populations of 2, 20, and 198 should be noted as occurring on a temperature of 74° F. and populations of 57, 6, 6, and 4 on a temperature of 73° F.

B—An ultraviolet-hydrogram for quail populations at Prairie du Sac using April ultraviolet and April rainfall. The actual populations are shown. The scale is one-tenth the actual population figures. A systematic series of readings from this figure covering a representative lot of combinations of ultraviolet and rainfall gave a correlation with rainfall of —.554 and a correlation with ultraviolet of —.014.

the plants studied is almost directly proportional to the intensity received up to about 20 percent of full summer sunlight. At higher intensities the slope of the curve falls off, shade plants showing a decrease at lower intensities than sun plants. The well-known relations of the growth of the Indian corn plant to temperature by Lehenbauer (see Shelford 1929, p. 181) is characteristic of temperature relations of practically all organisms. The application of radiant energy in the treatment of disease is based on dosages suggesting a similar principle. It is well known that there are also optimum moisture and rainfall conditions.

It has already been suggested there are narrow limits within which solar ultraviolet appears to be an effective stimulus to reproduction. Actually, however, we have only rough estimates of relative intensity in critical periods from year to year. It seems easily possible that the atmospheric conditions may be such as to reverse these periods in two years and make the year of higher astronomical intensity lower in a particular period than a year of low astronomical intensity. However, there is little evidence that this has happened with the periods under discussion. The summations at Cleveland trend in the same direction as the overlapping Pettit readings.

Something is known of the length of exposure to suitable ultraviolet necessary to cause reproductive stimulation. Marshall & Bowden (1934) used 360 ergs/cm^2 sec, at 365 mμ, 8 hours per day and secured results after 21 days; the control period was four months. Sabrosky et al. (1933) exposed the grouse locust to mercury vapor lamps continuously for four months. The period at a rather high intensity under indoor conditions strengthens the idea of concurrent action of moisture in nature when the periods are compared with the evidence as to periods in the out of doors. Both studies indicate that wave lengths longer than those measured for erythema are effective for reproduction.

The construction of hydrothermograms brought out the fact that such diagrams cannot be made for the prebreeding season in the vertebrates for using more than one month or apparently less than 15 days as the stimulation period. In the case of the chinch bug, two 30-day periods are the basis, but there is as much as 12 days between flight from hibernation to egglaying; after the first laying, there are several copulations, and eggs laid in several lots.

The evaluation of daily exposure in the quail or the chinch bug would be an extremely difficult task. In the case of the quail the time of exposure varies with the temperature (Stoddard 1946, p. 118), probably especially in the spring. The details of amount of exposure in relation to shelter for either of these species are difficult to imagine. However, the effective exposure is probably greatly increased by the fact that the eye and cephalic region are the chief receptors in the vertebrates (Marshall & Bowden 1934; Benoit 1935; Benoit & Ott 1938) and probably in the insects.

Luckiesh, Taylor, & Kerr measured wave lengths 335 mμ and shorter, maximum sensitivity of the phototube at 280 mμ. Coblentz & Stair measured 313.2 mμ and shorter; maximum sensitivity of the phototube not given. The difference in the apparatus and probably the treatment of the readings is the cause of the differences as expressed by the ergs required for erythema. Fig. 9 indicates the optimum

limits as between 887 milliwatt min/cm^2 and 737 milliwatt min/cm^2, a difference of 150 milliwatt min/cm^2 with the Washington apparatus (mean April-May sums). With the Cleveland equipment it would be about 25 milliwatt min/cm^2. Marshall & Bowden (1933) irradiated the ferret, a nocturnal burrowing animal probably with a low light optimum, at the rate of 518 milliwatt min/cm^2 per month or about 363 milliwatt min/cm^2 to secure results. Naturally none of the forest edge animals used in this discussion received all the recorded monthly irradiation. Above all, on the spot records are needed.

Both Luckiesh, Taylor & Kerr in 1936, and Coblentz & Stair in 1943, made readings during clear days and show curves from hourly readings. Their noon day results in milliwatt sec/cm^2 were as follows:

Cleveland—1936	Washington—1943	Ratio
April 13, 8.0	April 11, 114.0	14.25
June 15, 24.5	June 4, 180.0	7.34
Sept. 6, 17.0	Sept. 18, 90.0	5.29
	Dec. 21, 34.0	....

The April 1936 sum was 23% below the four-year April mean (1935-1938) while the April 1943 sum is 13% above the four-year mean (1941-1944). The 1936 April reading on the basis of 1943 would normally be about 20.0. This large reduction doubtless came about through large amounts of water vapor. The Coblentz & Stair (1944) curve of readings every half hour on April 11 amounts to approximately 37 microwatt min/cm^2 for the day. The mean per day for April 1943 was 26; April clear days should be about 32 microwatt min/cm^2. Approximately 15 per day is probably near the lower limit of good quail reproduction. This makes the optimal range about 11 microwatt min/cm^2. For the chinch bug available data do not make such estimates practicable. All figures are very rough, due largely to the very sharp decrease in ultraviolet between 330 mμ and 280 mμ (Pettit 1932, p. 219).

A provisional lower ultraviolet optimal limit is marked in Figs. 9, 10, 12, and 13. Less effect is indicated for conditions of ultraviolet below the optimal limits than above them. This is shown in 1932 for the chinch bug, Fig. 9; the quail at Prairie du Sac, 1932, Figures 13, 14A and B. There was an average ultraviolet ratio of 88 for April (101 suggested as the lower limit in Fig. 12) and 91 for May. There was a small decrease of quail in Ohio. However, there was a 1.5% increase at Prairie du Sac, Wis., where preceding winter losses were low and the birds probably in good condition. The 1936 ultraviolet low was accompanied by sharper decreases than 1932 and the upper limits appear to be fully operative in all the cases examined. In the case of 1936 there is a little evidence that high atmospheric transmission may have partially offset the low astronomical values in May (see Coblentz & Stair 1943, Figs. 4 and 5); no April readings are shown for 1936.

In his review of bird reproduction Burger (1949) states that "there is no evidence that ultraviolet is stimulating or necessary." The evidence here is that it is a stimulus to reproductive potential and probably to the vigor of the young in the grouse locust (Sabrosky, Larson & Nabours, 1933), and in the chinch bug.

It is strongly suggested by ultraviolet-hydrograms using April, Figs. 14A, 14B, and 16, that ultraviolet light and moisture are paired and operate concurrently. Another relation is brought out in the study of the butterfat of cow's milk (Shelford 1951). The isoropic lines do not form ellipses when relative humidity is used; each figure formed by equal value lines makes a "C" facing away from low humidity. It is generally agreed by most physiologists that absolute humidity (not available in weather records) is the effective moisture factor. Since vapor pressure increases rapidly with temperature increases, the role of temperature is evident (Robinson, et al. 1945). That moisture is effective in increasing reproductive potential is shown by study of the codling moth populations (Shelford 1927). In this case heavy October rains broke the diapause in the larvae and this was followed by more rapid development and larger populations, probably resulting from the diapause hormones being followed up by reproductive hormones which are stimulated by the presence of high vapor pressure and actual wetting of the larvae in the autumn. Wigglesworth (1948) has pointed out many important related hormonal phenomena but it appears that he has not discussed reproductive potential. In the case of the oxygen-carbon dioxide diagram, there is considerable basic knowledge of the relation the two have to haemoglobin. In the case of the hygrothermogram of the codling moth, temperature and moisture operated together as vapor pressure. A considerable number of thermohydrograms are concerned with equal death rates and the physiological basis of the operation of the paired factors is fully as obscure as is the relation of moisture to the stimulating effect of light on the hormone system.

The advantage of the discovery of paired factors is evidently great because they appear to represent 85% to 90% of the total effect of external physical factors. This leaves several factors with a very minor role.

The application of the usual statistical methods to those data which fall into the form of, e.g., thermohygrograms do not seem satisfactory and probably some method of dealing with them should be devised. The use of double correlation may be tested with that portion of the codling moth thermohygrogram which would be effective in a two-week period of above normal August temperatures in the southern Illinois apple belt (Fig. 18A). The portion of the thermohygrogram used is shown by the heavy lines in Fig. 18A. The systematically chosen set of rates covering temperatures and humidities ranging from 70° F. (21° C.) to 104° F. (40° C.) and 10% (two items only) to 100% relative humidity were used. Developmental rates ranging from 10 to 21 were available. These data gave a correlation between rate and temperature of 0.10; between rate and humidity of 0.32. In fact, the relation involving temperature is about half negative. The rates go

up as the temperature is raised to about 88° F. (31° C.) or 90° F. (32° C.) depending on the humidity and then decline rapidly within life limits. The correlation with humidity comes about in connection with humidities below 45%, which occur near midday in hot dry weather and are probably less frequent than the systematically selected rates used would indicate. It is probable that under most hot weather conditions the correlation between rate and humidity would be no greater than that between rate and temperature.

When the entire chart was tested for correlations, the correlation of rate with humidity was 0.03 and with temperature 0.73. About one-fourth of the chart is negative; otherwise, the correlation with temperature would probably have been almost 1.00. A third test was made of the complete thermohygrogram of the first instar of the chinch bug, which is rather unusual as regards the effect of humidity. The correlation with a representative set of rates taken from this chart was determined. The correlation of rate with temperature is 0.25 and with humidity is 0.63. The low temperature correlation results from about one-half of them being retarding or negative.

These correlations under out-of-door temperature and humidity conditions can never be depended upon in case of cold-blooded animals unless there is a very large expenditure of labor to secure accurate hour-to-hour records of conditions. Since population studies must be carried on for periods of years such records are not very feasible. Mean values of conditions must usually be used. The lack of reliability is caused by the following:

1. The daily means give no indication of the occurrence of humidities or temperatures which have retarding or negative effect and no indication of simultaneous occurrence of certain temperatures and humidities.

2. Still more important is the daily march of temperature and humidity (Shelford 1927, p. 389-397; 1929a, p. 277; 1929b). Fig. 18B shows, in the case of the chinch bug first instar, that if the daily march tends to pass hour by hour, from temperature 20° C. (68° F.) and humidity 90% to temperature 40° C. (104° F.) and humidity 30%, the correlations will be quite different from those derived from a daily march from 20° C. (68° F.) and 95% to 38° C. (100.4° F.) and 95% on a rainy day.

Figure 19A shows the distribution of population of overwintering chinch bugs per m^2 in Trelease Woods and a humidity temperature chart for August, 1933 through 1947. The correlation with temperature was 0.40, though populations of 2, 20, and 189 occurred at temperature of 74° F. (23° C.) and, of 57, 6, 6 and 4 on 73° F. with correlation with humidity was 0.00. No thermohygrogram can be drawn for this population (see Huntsman 1949).

Figure 19B, we may consider the ultraviolet-hygrogram of the quail at Prairie du Sac, Wisconsin, 1928 to 1941 (Errington 1945). The rainfall data are for the month of April, which is the breeding season. The vertical scale is Pettit's ultraviolet light indices and the data on which the ellipses are based are the population for the several years (see Fig. 14). The ellipses have been completed, smoothed and 50 smaller proportional figures substituted for actual population figures. The correlation with ultraviolet was found to be −0.014 and with rainfall −0.554. This indicates that if the relationship of the quail and its population to the two factors—moisture and ultraviolet light—suggested by the diagram were established, the usual type of correlation studies would indicate very little of significance.

The usual year-to-year graphic representation of populations usually indicates a correlation with some of the weather factors when plotted with reference to sensitive periods of the organism's life history which are usually unknown to the statistician. The doubtful factors (e.g., ultraviolet) may be tested by plotting them with reference to an evidently important one after the manner of Figs. 10 and 13. In these cases population size is assumed to result from ultraviolet-concurrent moisture stimulation of reproduction, modified by mortality due to the paired factor, namely rainfall. With a large series such as may be acquired in fifty to one-hundred years of population records, many of the difficulties of the statistician will be eliminated. This is true especially if close life history studies of all the species should accompany population studies and experimental work with both constant and variable temperatures, and out-of-doors checks are carried out.

X. SUMMARY AND CONCLUSIONS

(1) Seven species of invertebrates which come into the woods for the winter were studied; six are discussed. Chinch bug populations were considered back to 1823 for comparison with our collections The bob-white quail, a forest edge bird, and the cottontail rabbit, a forest-edge mammal, both of which frequent the woods in winter, were considered back to 1925 from published data.

(2) The populations of different animal groups show a series of peaks as follows: non-forest invertebrates 1934 and 1944, forest invertebrates 1937 and 1945-47, and birds and mammals at intermediate dates (Fig. 3).

(3) Correlations of populations with physical conditions are referable to sensitive periods in life histories. Sensitive periods most often fall in some of the spring months especially April, May, or June. In some birds and mammals February or March is important (Fig. 17). The month before mating or before young or eggs are produced is the period in which short wave radiation appears to be an important reproductive stimulus.

(4) Populations of several non-forest species show obvious correlations with rainfall in year to year graphs; direct correlations with temperature are not usual.

(5) Moisture appears to be paired with intensity of ultraviolet light as the chief control of population size in several species studied. Population diagrams

based on intensity of ultraviolet and moisture form equal population lines in the form of a system of concentric ellipses which resemble thermohygrograms for temperature and humidity and rate of development (Figs. 14, 15, and 16).

(6) The quail and chinch bug populations, 1925-1941, show obvious correlations with an optimum intensity of solar ultraviolet in April and May for the chinch bug and April for the quail, particularly on Pettit's scale (Figs. 9 and 12).

(7) The rabbit populations are related to February ultraviolet light and rainfall later in the year (Fig. 17).

(8) The populations of the chinch bug were analyzed with reference to the solar phenomena including sunspots and weather conditions from 1823 and in detail 1866 through 1947. Chinch bug population peaks have occurred when sunspots were increasing and again when they were decreasing in accord with the supposed associated ultraviolet intensity based on the operation of the ozone screen. A few increases have been absent in relation to the annual sunspot decline, e.g., in 1940. In no case has a population peak occurred at the time of a sunspot maximum (Fig. 11).

(9) The population peaks shown in Fig. 3 cannot be expected to recur even if correlated with ultraviolet light, because of (a) variations in intensity or (b) adverse weather or (c) unpredictable variations in solar phenomena.

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FLUCTUATION OF FOREST ANIMAL POPULATIONS IN EAST CENTRAL ILLINOIS

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I. INTRODUCTION

Published figures on variations in the size of plant and animal populations have been derived far too largely through reports on the sale of furs, crop production, and insect outbreaks. Furs are frequently held off the market and insect pest populations are commonly neglected when damage is slight. The study to be described was made on a population subject to a minimum of human interference. The objective was to ascertain the size of the populations from year to year and attempt to correlate them with observable physical factors and conditions of the vegetation.

About half of the main body of the paper is devoted to methods of sampling forest invertebrates. It will be shown that the samples in themselves, when taken in adequate numbers, can be used as indicators of their validity by the demonstration of winter losses, and responses to weather conditions at the time of collection. Only a little attention has been given to statistical analysis, largely because only 13 or 14 items are available.

The second half of the paper is largely devoted to pointing out correlations with physical factors, chiefly rainfall. It will be shown that such correlations can be made only when the sensitive periods of the life history are taken into account. On this basis, variations in population size of a number of species and groups of species have been followed in some detail though in most cases no essential specific physiological conclusions are possible. This detail is designed to serve the important function of emphasizing the heterogeneity of sensitive periods in life histories which, in a mixed population, extend to nearly every week of the year and involve indescribable places in which stimulation may occur or fail to occur. With the emphasis on sensitive periods, the detail is fully justified.

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1. Location

The study was conducted in a remnant of a 10-square mile (26 km^2) grove of deciduous forest. The grove was somewhat triangular in shape and had its center near 40° 8′ north Latitude and 88° 9′ west Longitude. At the time of its settlement, the general region was characterized by groves and stream-skirting forest in an area predominantly prairie. The triangle was about 50 miles (80 km.) west of the main body of the forest at the latitude given above. The climax forest appears to be red oak-sugar maple.

The remnant used for the study is an approximately 60-acre tract in Champaign County, Illinois, five miles E.N.E. of the University of Illinois campus. It is known as the William Trelease Woods. Its size is reduced by a highway on the west side, by a drive and fire break around the entire area, and by an unwooded corner, leaving about 50 acres (20 hectares) with trees of more than 10 in. (25 cm) in diameter at breast height.

This forest remnant was for a long time the property of a local family whose representatives have stated their their aim was to keep it essentially virgin. Only occasional trees were removed during nearly 80 years of their ownership. A few walnut trees were removed for gun stocks late in the period of the first World War. It had been completely protected for fifteen years when the study began.

2. Climate and Weather

The average rainfall in the area is 36.5 in. (92.7 cm) and the mean annual temperature is 51.6° F. (10.9° C.). The mean annual humidity is 71% (15 year average, 1933 through 1947). Details of differences in portions of the growing season will be brought out in connection with the description of population changes. Usually there is some snowfall each month, November through March. In a 15-year period, a trace to 14 in. (35 cm) in any one of the winter months is to be expected. The annual total may range from 5 in. (13 cm) to 32 in. (81 cm) in any single year. There is usually a trace and occasionally a snowfall of 5 in. (13 cm) or more in April, which is unimportant and usually melts within 48 hours. The rare October and May snowfall is generally without significance. The year to year and month to month normal differences and variations in weather conditions will be discussed in connection with the variations in populations and related matters.

The U. S. Weather Station on the University of Illinois campus is five miles from the Trelease Woods. Differences between records at this station and the records of instruments in the woods are important. However, the weather station reports had to be used over much of the period of study because of imperfections in the records of some operators, failure of instruments, etc., at the woods station.

Two rain gauges were placed about 20 ft. (6 m) apart near the center of the woods. The more northerly one nearly always showed the higher reading, in a few cases as much as 0.4 in. (1 cm) more than the other one. This figure represents differences in the amount of rain intercepted and deflected by foliage and running down the limbs and trunks of trees adjacent to the two gauges. There was appreciable evaporation from the gauges between weekly readings.

The rainfall records in the woods were best during a part of the period from January 1, 1939, through May 31, 1942. In 1939 only two weeks showed more rain at the woods than on the campus; for the year the woods showed 79% of the total for the campus. In 1940 there was more rain at the woods for five weeks, and the woods showed 88% of the total for the campus; in 1941, more rain at the woods for five weeks, and 76% of the total for the campus. The total at the woods for the three years in which records were made during the winter showed 81% of the total for the campus. This indicates that 12 to 24% of the rainfall may be diverted by the canopy. Because of lack of a gauge adjacent in the open field, the figures give only a rough idea of what may be expected. Beall (1934) found that the rainfall average recorded by four gauges in an Ontario hardwood forest was 79% of the rainfall recorded by a gauge in the open. (See also Clark 1937, Hauk 1929, Horton 1919, Mitchell 1930, Ney 1894, Simson 1931, Wood 1937.) Clark (1937) studied the interception of rainfall by herbaceous vegetation and showed it to have considerable bearing on the conditions of the soil and litter, while Voth (1939) found conduction by plant stems to be an important factor. It has been assumed that almost none of a rainfall of 0.01 to 0.05 inch would reach the soil or litter. (See also Hartzell 1916.)

Drought periods have been demonstrated by this study to be important in ecological relationships. (See also Munger 1916.) Intensity of drought is expressed by the length of the period of days with little or no rain. On the basis of rainfall records, periods of eight or more days with a total of less than 0.1 in. (2.5 mm) and fourteen or more days with a total of less than 1 in. (25.4 mm) were designated as dry periods (see Fig. 10).

Weese (1924) and Jones (1941) found atmospheric humidity important in the life histories of

insects and spiders. Our records for the woods humidity are not good in an over-all sense because of difficulties in standardizing and maintaining the Friez hygrographs in accurate operation. Some of the records, 1937 through 1940, were excellent and could be compared with those of the University of Illinois weather station. The selection of records for this purpose was made on the basis of both instruments reading 99-100% when rain was falling at the same time in both places (Fig. 1). Sections were chosen which were followed or preceded within one or two days by precipitation. Readings were made from the charts by two-hour periods and then corrected when necessary to the basis of 99-100% of saturation. Fig. 1 shows that the 2 P.M. to 4 P.M. readings in August were as much as 50% lower in the open than in the woods. In fall and early spring these differences appeared to be somewhat less. In midwinter, with temperatures varying from 10° or 15° F. above and below the freezing point from day to night, the differences were about 10%, the open weather station being lower for several hours on each normal day (see Fig. 1—Jan., 1938) but higher near sunrise and sunset. The rapid conversion of water to water vapor during periods of sunshine in winter, especially when snow is on the ground, is well known. The result is a rapid increase in percentage of saturation with the appearance of clouds and at sunset. This is brought out in the Jan. 3-4 curve of Fig. 1, where the weather station reading exceeded that of the woods four times in 36 hours. The woods series had many gaps, and reliable average differences between the woods and the weather station could not be made. The reader is left to note differences in April, June, August, and October, as shown in Figure 1.

Account has been taken of the amount of sunshine. For this purpose the U. S. Weather Bureau records for Peoria, Illinois, 70 miles W.N.W. of Urbana, and for Springfield, Illinois, 65 miles W.S.W. of Urbana were averaged to give the best available approximation of percentage of possible sunshine. Attention has also been given to ultraviolet light intensity as measured on Mount Wilson, 1924 through 1938 (Pettit 1932; Int. Ast. Union, 1924-1938), at Cleveland, Ohio, 1934 through 1941 (Luckiesh 1946), at Washington, D. C., 1941 through 1944 (Coblentz 1945), and to sunspots with which ultraviolet light is only very roughly correlated. This was discussed in another paper (Shelford 1951). Various devices or diagrams commonly called climographs covering the year, or portions of the year, have been used to illustrate combinations of temperature and rainfall, sunlight and rainfall, etc.

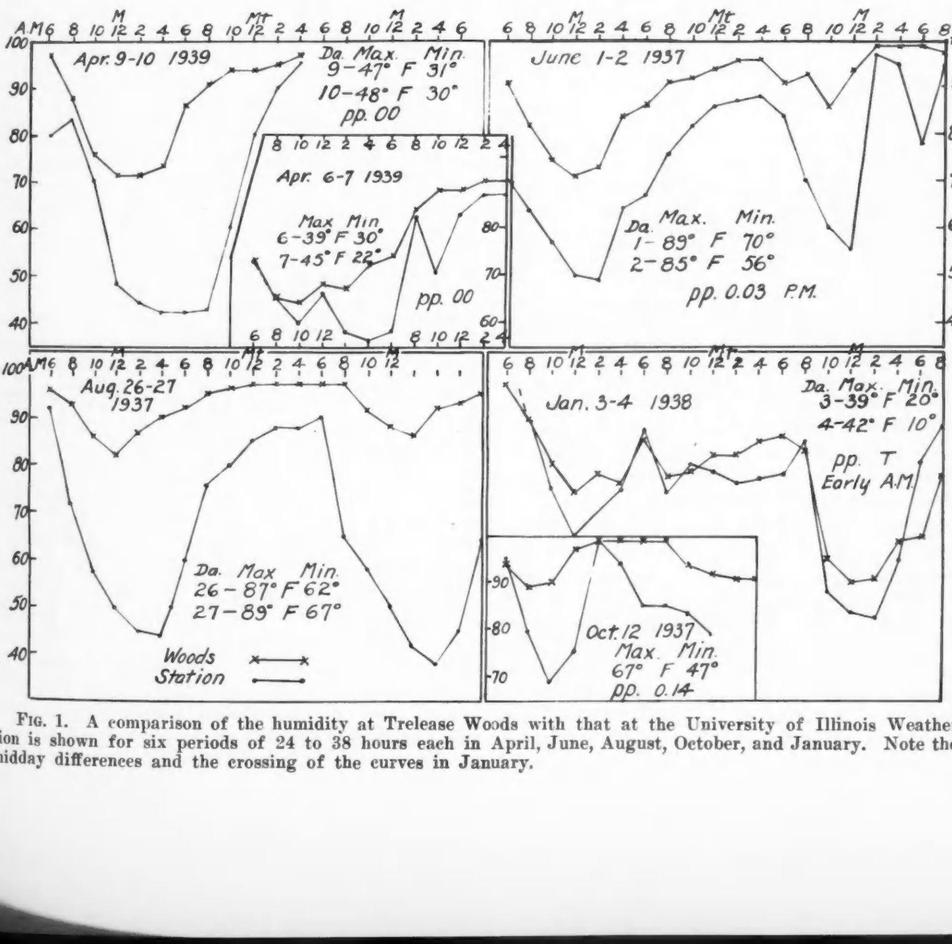

FIG. 1. A comparison of the humidity at Trelease Woods with that at the University of Illinois Weather Station is shown for six periods of 24 to 38 hours each in April, June, August, October, and January. Note the wide midday differences and the crossing of the curves in January.

II. THE BIOTIC COMMUNITY

1. The Forest Vegetation or Plant Constituents

The principal forest trees of the area are listed below with their relative abundance indicated as percentage of the total basal area, as given by Vestal & Heermans (1945):

Sugar maple (*Acer saccharum* Marsh) 28.5%; American elm (*Ulmus americana*, L.) 18.1%; basswood or linden (*Tilia americana* L.) 9.6%; slippery elm (*Ulmus fulva* Michx.) 9.4%; white ash (*Fraxinus americana* L.) 7.0%; red oak (*Quercus borealis* Michx.) 7.0%; buckeye (*Aesculus glabra* Willd.) 6.2%; black walnut (*Juglans nigra* L.) 4.5%; burr oak (*Quercus macrocarpa* Michx.) 2.9%; hackberry (*Celtis occidentalis* L.) 2.6%; blue ash (*Fraxinus quadrangulata* Michx.) 2.5%; and yellow oak (*Quercus muhlenbergii* Engelm.) 1.8%. The less abundant trees are two species of hickory, hawthorn (*Crataegus mollis* (T. & G.)), honey locust (*Gleditsia triacanthos* L.), mulberry (*Morus rubra* L.), and some additional oaks.

The herb and shrub vegetation of the higher ground of the woods where samples were taken is a typical subordinate climax community of fairly uniform composition. The shrubs and shrub-sized trees on 1000 m^2 of the area late in June, 1947, are listed, followed by the heights in meters and the number of individuals respectively: pawpaw (*Asimina triloba* (L) Dunal) (0.5-3 m) 142; spice bush (*Lindera benzoin* (L) Blume) (1-3 m) 22; basswood (*Tilia americana* L.) seedlings (1-3 m) 12; sugar maple (*Acer saccharum* Marsh) seedlings (0.5-3.0 m) 10; Ohio buckeye (*Aesculus glabra* Willd.) seedlings (1.5-3 m) 8; hackberry (*Celtis occidentalis* L.) seedlings (1.5-3 m) 7; blue beech (*Carpinus caroliniana* Walt.) (1-3 m) 5; ash (*Fraxinus* sp.) seedlings (1-3 m) 3; hickory (*Carya* sp.) seedlings (2 m) 2; hophorn beam (*Ostrya virginia* (Mill) Koch) (1 m) 1. Number of shrub and tree seedlings vary from year to year.

In making collections of invertebrates by "sweeping" herbs, in a woods, the collector cannot avoid striking some small shrubs and tree seedlings, even though he exercises great care. An observer following a person who was "sweeping" recorded five to twenty small shrubs, vines, and tree seedlings hit by 48 net strokes. Usually a person in making 48 net strokes will travel 40 to 48 meters, and a count of herb-sized woody seedlings along a 1 m by 48 m strip gave the following list: pawpaw, 8; hackberry, 2; maple, 2; buckeye, 2; ash, 1; spice bush, 1; and Virginia creeper, 1.

A 48-meter transect 1 meter wide on the study area (June 20, 1947) showed the following herbs and herb-sized woody seedlings; the number of individuals follows the name: water leaf (*Hydrophyllum canadense* L.) 323; nettle (*Urtica procera* Muhl.) 228; bedstraw (*Galium* sp.) 67; unidentified fern, 64; sanicle (*Sanicula gregaria* Bickn.) 62; wild ginger (*Asarum reflexum* Bickn.) 56; sedge (*Carex* sp.) 46; jewel weed (*Impatiens* sp.) 14; false Solomon's-seal (*Smilacina* sp.) 14; sweet cicely (*Osmorhiza claytoni* (Michx.) Clark) 14; yellow violet (*Viola eriocarpa* Schw.) 9; grass (*Hystrix patula* Moench.) 9; grass (*Festuca obtusa* Spreng.) 6; water leaf (*Hydrophyllum appendiculatum* Michx.) 5; sugar maple seedlings, 5; pawpaw (*Asimina triloba*) 4; Virginia Creeper (*Parthenocissus quinquefolia* (L.) Planch.) 2; hackberry seedlings, 2; spice bush (*Lindera benzoin*) 2; (*Geum canadense* Jacq.) 1; red bud (*Cercis canadensis* L.) 1; buckeye, 1; and oak, 1; a total of 936 herb-sized plants.

2. The Animal Constituents

The animals considered in this paper are species which appear to be exclusive forest dwellers in the region of study. Some species or groups which cannot be readily sampled are not considered; they include Collembola, small soil mites, red earthworms, white earthworms, soil ants and all species and forms that cannot be counted with the naked eye. This is because special techniques are required to evaluate populations of some of them or because the methods used do not give good samples on account of vertical migrations below the 7.5 cm downward limit of soil collections. Soil ants cannot be properly sampled with the soil ring on account of their colonial habits and lack of uniform distribution. Species with a preference for fallen logs and the exclusive tree bark inhabitants have been taken only incidentally.

Approximately 500 species of invertebrates have been collected in the woods and identified by specialists. Some sort of report on 50 of these is included here and in addition the following categories or combinations have been used: (a) total population, (b) total population of field species, (c) total population of woods species, (d) herb and shrub population, (e) soil population, (f) herb and shrub spiders, (g) herb and shrub ants, (h) mollusks, (i) millipeds, (j) centipeds, (k) crane flies, (l) crane fly larvae, (m) dipterous larvae, (n) total Diptera, (o) Melanophthalma, several species, etc.

The millipeds, most of the centipeds, the mollusks, and crane flies consist of strictly forest species. Insects and spiders present species which show a greater variation of habitat selection. Their motility has enabled some of them to move from forest to crops that are short stemed as compared with trees and evidently to live under physical conditions similar to those found in the forest. For example, *Acrosternum hilaris* Say, a common green stink bug that in Trelease Woods shows a preference for shrubs but that has a population there too small for population variation studies, is a serious crop pest in Virginia. *Jalysus spinosus* (Say), the common stilt bug of Illinois woodlands that occurs on the herbs in Trelease Woods, is an alfalfa inhabitant in eastern Kansas (Smith *et al.* 1943; Metcalf & Flint 1939). In both cases the physical condition in the field habitats concerned are known to be similar to those in a forest. Non-forest species show reactions

to weather conditions different from those of the forest species (Shelford 1951).

In evaluating populations it is necessary to understand the life histories of the animals under consideration or the prevailing life history type in an aggregate population. Unfortunately, however, life cycles are too often uninvestigated. The vast majority of organisms considered, both plant and animal, are of so little economic importance that studies of their life histories are not found in scientific treatises, agricultural bulletins, etc. (Smith-Davidson 1932).

On the basis of life histories, the forest animals fall into several classes.

First, animals which live approximately two years or more, so that a continuous adult population is present. Included in this class are the resident birds, the mammals, and a few invertebrates such as millipeds of the genera Fontaria and Spirobolus (Hanson 1948). Also included in the two-year class are mollusks and perhaps centipeds. The mollusks reach maturity slowly, but may be recognized as to species before maturity. Some minute snails may live only one year. Barring young stages of millipeds the species having the greatest effect on total populations are one-year species. The young develop rapidly and when conditions are favorable often increase sharply. Species with this type of life history are by far the most abundant and fall into the second and third categories.

Second, animals which pass the winter in the egg stage or other immature stages. Among these animals are a large number of insects and spiders with one generation per year (Jones 1940, 1946).

Third, animals which pass the winter as adults and deposit eggs in the spring with the old and new generations overlapping. Included in this class are a few Heteroptera, most Coleoptera, a few Lepidoptera, and some one-year millipeds.

Fourth, animals which produce more than one generation per season. No forest invertebrates of this type have been studied. They are probably limited mainly to such groups as aphids and coccids. However, some of the small rodents belong in this group.

Fifth, summer resident birds which are present during the breeding season, the young and adults both leaving at its close. They frequently return to the same locality for breeding in succeeding years.

Sixth, animals that have life histories the duration of which is not ascertainable. These are best exemplified by ants.

The vertebrates have been studied by several different investigators. Birds were censused by Blake (1926) in 1924-25, by A. S. Hyde 1926-29, who did not publish his results (Kendeigh 1944), by Twomey (1945) 1933-1936, and by Kendeigh (1944, 1948) who is still following them. E. J. Koestner (1939) made an especial study of the fox squirrel. This study was carried to 1947 by the use of nest counts. Lindeborg (1941) made a three-year study of mouse populations; this study has been continued by Kendeigh.

III. SAMPLING, LOCATION, AND METHODS

1. Location Within the Woods

The Trelease Woods is marked off into 50 m quadrats by permanent, numbered stakes. The invertebrate collections were made almost exclusively on an area consisting of a block of four quadrats making an area of one hectare; its southeast corner is at the center of the woods. No collections were made less than 100 m from the edge of the woods.

2. General Methods Applied to Invertebrates

The two principle methods are concerned with soil and litter samples and with samples from the herbs and shrubs.

A. THE SOIL-SAMPLING METHOD

First method, a steel ring 3 in. (7.5 cm) wide with an area of 0.1 m^2 was pressed into the soil, and litter and soil within the ring were removed. In the earlier years of the study the animals were removed and counted in the field whenever weather permitted. This was because of the difficulty in transporting the soil back to the laboratory. Beginning in the summer of 1942 all soil was transported to the laboratory for examination. In winter especially, wet soil was stored at 6-8° C. for several days before it was examined to permit evaporation of excess water. The soil animals and litter animals were counted together. Since about 1944, the litter and soil have been kept separate to facilitate examination. The litter was put into a Berlese funnel and the animals obtained were listed with those of the soil. A Morris soil washer (Morris 1922) which uses water running through three sieves was tried with two samples, but losses of individuals were obviously serious. The soil sampling was improved over the period of study; the changes modified the total of the collections in a minor way but did not change the counts of the larger forms referred to under their generic names.

The methods of sampling used in the first two years of this study differed somewhat from that described above. In these years, soil samples were taken from a sq. ft. area measured on the surface of the soil and 50 sweeps of the net were used (Rice 1946). If a ring is not used and an area is only marked on the soil, there is a tendency to exceed this area, also the digging is usually less definite as to depth. When these larger sample are used in the calculation of population indices there is a tendency for the two additional sweeps of vegetation (50 instead of 48) to be offset by the smaller area of the soil samples.

Care was used to avoid selecting soil samples from spots close to those sampled only a short time before. Net collections were not repeated on the same transect (1 x 48 m) for a considerable period of time although Rice (1946) demonstrated that complete repopulation of the swept areas occurs in a few days.

B. THE SWEEP-NET METHOD IN HERBS

The second principal sampling method involved the use of the standard sweep net; a net with a ring

13 in. (33 cm) in diameter and a sack 24 in. (61 cm) deep. The catch of 48 strokes on the herbs and on the shrubs were used as representing the population above a square meter of ground.

Weese (1924) used ten sweeps of a net of the same size as used in this study, each stroke 1.0 m in length, to give a sample equal in numbers to the population on a square meter of vegetation.

Shackleford (1929), working on a relic prairie, inserted an inverted cylindrical can of known diameter into the soil at a period of insect inactivity and killed all animals under the can with an anesthetic and compared the numbers of abundant animals recovered with the number taken with a certain number of rapid strokes of the sweep-net. Such species as *Lygus oblineatus* Say were especially useful for this purpose. These studies led her to use 50 short strokes to represent the animals on the vegetation of a square meter. Smith (1929), who worked with Shackleford, used the same criteria, but only a part of Smith's work was with forest similar to the area of study.

The nets mentioned in this section are all of the same construction and supposed dimensions. However, the opening is not completely round and the variation in stiffness of the spring steel strips which make the ring cause the diameter of the opening, which actually strikes the vegetation, to vary in different nets or even in the same net, with continued use.

Again, Beall (1935) used the same type of net measuring 32 cm (12.8 in.). His strokes were 2.5 m long and with about six of these long strokes he collected a population that approximated the population of a square meter. Employing statistical methods of analysis of population densities, he concluded that sweeping is a valid method for comparing populations on different dates. (See also DeLong 1932.)

The initial work on methods of collecting in the woods was done by Rice (1946), following Shackleford's general methods of sampling grassland vegetation. She determined the effectiveness of sweeping Using 125 strokes on 400 square meters, she found that by sweeping the area four times in rapid succession the number of individuals was reduced from 237 in the first trial to 88 in the fourth (August 8), and from 223 to 33 (August 18) (Rice 1946, p. 156, Table 1). The Hemiptera, Coleoptera, and Diptera declined with each succeeding trial on both dates. Spiders declined regularly on the first date but irregularly on the second date. Ants, snails and Homoptera declined irregularly or they were very few in number on the first date but declined regularly on the second date. The Homoptera on the first date showed no change with repeated sweeps, indicating that they were taken on the wing. On the second date there was only a slight decrease with repeated sweeps.

For the study described here, the sweep-net was swung on a 4 ft. (122 cm) radius at the rate of about one stroke per 0.8 m of advance. The sweeps were made in rapid succession, with the direction of each stroke away from the foot being moved forward, until 48 sweeps were made.

Sweep collections may be placed in heavy paper sacks and anesthetized. They must be processed as soon as possible after being taken, not later than on the same day. Each leaf must be examined on both sides. It takes about two hours to process and record each 48 sweep collection from the herbs and one and one-half hours for a collection from the shrubs. If the leaves are allowed to wilt and moisture to accumulate, 10% or more of the specimens may be lost. Examination of only one side of the leaves plus wilting may lose 20% of the catch.

Two observers following the sweep-net operator in the Trelease Woods determined the average penetration of the net into herbs 50 cm high to be 25 cm (20-30 cm) at its deepest point. The net first hit the vegetation 70 cm from the center of the stroke; therefore, the length of the chord was 140 cm. The area of the segment of the circle thus described within the mass of the plants was somewhat less than 2666 cm^2; the volume of the portion of the torus delineated was approximately 62,500 cm^3. Similarly, in vegetation 12 cm tall the net penetrated about 6 cm and the volume of the sweep area was about 4,800 cm^3. Eight strokes into the higher vegetation or 25 strokes into the lower vegetation included the volume of the vegetation on a square meter, yet nearly 48 sweeps were found to be necessary to sample a m^2 area in either case based upon many repetitions of Shackleford's (1929) method. This probably was due to the much more concentrated population in the upper half of the low vegetation than in the upper half of the taller. The only time all the vegetation is low is in early spring. In the summer a few strokes were regularly made on the patches of low vegetation. The first six sources of error noted below primarily for the 50 cm herbs apply also, with some modification, to low vegetation.

The following factors interfere with the above described mechanical operation of the net in herbs: (a) The greatest number of animals is in the upper half of herbaceous vegetation. (b) Many individuals are knocked to the ground and not caught. (c) Some individuals take flight on the approach of the net. (d) Insects in flight in the air are caught as the net is in motion above vegetation. (e) The animals are not uniformly distributed with reference to particular square meters. (f) In the sweeping of the herbs and shrubs, quantities of leaves and portions of plants are broken off and may at certain seasons fill the net to a degree which interferes with the number of individuals trapped. (g) All net strokes may not be on vegetation of the prevailing height.

C. THE SWEEP-NET METHOD IN SHRUBS

The same method of analysis cannot be used with respect to operation of the net in shrubs. The suitable foliage in the shrub layer was swept at a height of one to three meters. The strokes were aimed to represent the relative abundance of the dif-

ferent shrub-sized species, including six strokes of buckeye and six of basswood to secure the two species of lacebugs (species of Corythucha and Gargaphia). These twelve have been made regularly since 1942, and were made with less regularity earlier. Estimates by rough measurements indicate that there was shrub foliage of a thickness of one meter that covered the entire area of the type sampled. This statement does not apply to the entire area of the woods but to about 13 of the 20 hectares. The efficiency of the sweeping has to be judged by comparison with work on the herbs.

The trees present a different problem. The crown of this woodland is estimated to cover 90% of the surface involved. The trees range from 80 to 95 ft. (24-29 m) in height. The crowns of the maples, elms, and oaks, in the main, resemble inverted cones sometimes only slightly curved on top with foliage limited to about 13 ft. (4 m) of branch tips; where the trees are far apart, the layer of foliage that curved down for varying distances around the border of the crown. Some crowded trees resemble inverted truncated cones at the top. In some cases, especially in buckeyes, the foliage forms a narrow cylinder, rounded at the top, and coming down almost to within reach. The buckeye in the area of sampling are small; however, this feature is not of great importance because the depth of the foliage is less than in other trees. Observations made in the fall of 1947 with a forester's hypsometer and a 100 ft. tape were especially favored because the leaves of many large trees had not fallen on December 1, while all leaves of vines, shrubs, seedlings, and small trees had dropped. The dense foliage was confined to the outer 3 m of limbs in oaks, elms, and maples, but to only about 2 m in ashes and buckeyes. No doubt a few of the leaves of minor and lower branches had fallen, but it was evident that the dense top foliage remained. It was estimated on the basis of these measurements that the normal dense foliage averaged 13 to 20 ft. (4 to 6 m) thick throughout the 20 hectares. The 4 m of tips turning down on the sides of the crown were regarded as compensating for 10% of open sky. Seven hectares had very few shrubs, but, in an estimate of the population of the 20 hectares, the small trees of the entire area that were too large to be swept as shrubs probably compensated for foliage deficiency in the seven hectares.

D. OBSERVATION COUNTS

Another method, which may be called observation counting, was introduced as a further check on methods used. A heavy wire ring which enclosed a square meter was held by a handle about 18 in. (45 cm) above an area of herbs. The individual herbs included in the square meter were counted and located. Animals flying on the approach of the observers also were counted. One observer stood erect and observed from above and took notes. A second observer lay on the ground and viewed the under side of the foliage to ascertain kinds and numbers of animals and carefully removed one plant at a time until a square meter had been covered. A third observer aided in counting from above.

3. ADEQUACY OF SAMPLING

To check the validity of the sampling, considerable work was done from time to time in the summers of 1945, 1946, and 1947.

A. GENERAL PROCEDURES

In the 1947 work designed to test the validity of sampling methods in the field, the following categories were used, ranging from identifiable species to families and orders. They are to be distinguished from a list of more accurately determined species, etc., used in other parts of the discussion. Three categories for unidentified minute forms were included. The use of the larger categories is believed to be justifiable for the quantitative comparisons when sampling by different methods is employed at nearly the same times and places under nearly uniform environmental conditions, especially since a single species included in the larger categories often makes up most of the catch. In the course of a season, some species belonging to some of the categories no longer occur and new ones come in. In the following list of categories, strictly June categories are marked *, strictly September and October categories with †.

1.	Wedge beetles	*Anoplitis inaequalis* (Web) (many)
2.	Cantharid beetles*	*Cantharis* sp.
3.	Striped cucumber beetles	*Diabrotica vittata* (Fabr.) (few)
4.	Small black flea beetles†	*Epitrix brevis* Sz. (chiefly)
5.	Green leafhoppers (large)	Cicadellidae
6.	Small brown beetles†	*Melanophthalma* sp. (Chiefly)
7.	Click beetles	*Athous brightwelli* (Kirby)
8.	Brown leafhoppers	*Phlepsius irroratus* (Say) (chiefly) *Osbornellus aurontieus* Prov. (some)
9.	Leafhopper nymphs (large)	*Chlorotettix lusorius* (O. & B.) and *Gypona* sp.
9a.	Total leafhoppers	
10.	Green dolichopodid flies	*Sympyncus lineatus* Loew (?) (several)
11.	Bronze dolichopodid flies†	*Condilostylus* sp. (?) (several)
12.	Pale yellow flies	*Homoneura incerta* Mall. and *H philadelphica* Macq.
13.	Red eyed flies*	
14.	Tussock caterpillar	Lymantriidae (few)
15.	Other caterpillars	Miscl. Lepidoptera (few)
16.	Stilt bugs	*Jalysus spinosus* (Say) (few)
17.	Nabids or damsel bugs	*Nabis ferus* (L.) and *N. sordidus* Reut
18.	Assassin bugs and nymphs	*Zelus exsanguis* (Stal) (few)
19.	Stink bugs	Pentatomidae (few)
20.	Negro bugs	Cydnidae (few)
21.	Forest mirids	*Dicyphus vestitus* Uhler (very few)
22.	Tree crickets	*Oecanthus angustipennis* Fitch (chiefly)
23.	Walking sticks	*Diapheromera femorata* (Say) (?) (few)
24.	Yellow moths	*Heliothis armigera* (Hubner) (?) (few)
25.	Other moths	Lepidoptera (few)
26.	Lantern flies†	*Ormenis* sp. (few)
27.	Green legged spiders	*Mangora gibberosa* (Htz.)
28.	Crab spiders	Thomisidae (few)
29.	Other spiders	Attidae and Agelenidae (chiefly)
29a.	Total spiders	Araneida (many)
30.	Harvestmen	*Leiobunum* sp. (few)
31.	Ants (several sp.)	Misc. Spec. (several) *Leptothorax curvispinosus* Mayr. (few)
32.	Snails	*Mesodon thyroidus* (Say) (chiefly)
32a.	Pupoid snails	*Vertigo ventricosa* (Say) and *Carychium exile* H. C. Lea
32b	Helicoid snails	*Retinella indentata* (Say) and *Hawaiia* sp.

33. Miscl. Hymenoptera.........Ichneumonidae and Braconidae
34. Miscl. Diptera...............Mycetophilidae and Psychodidae (many)
35. Small nondescripts White flies, chermids aphids, etc. .....Aleyrodidae, Chermidae
Aphididae, some small
Cicadellidae especially small white ones and green ones
Cynipidae, Chalcidae, etc., (many)

An inverted cylindrical can, covering a square meter, was constructed. Usually it was operated by being lowered from a rope stretched from between two trees. On September 20, 1945, Auerbach secured 92 individuals in 48 sweeping strokes and picked up 72 (82%) under the can. In this case the can was thrown into place by two men at 4:30 A.M. (Auerbach 1949). One late autumn can collection contained very few animals, but there was good agreement between 48 strokes of the net (86%) and the one m² can collection as regards several species known to habits (Table 1). In 1947 a series of checks were made in June when can collections from four square meters were compared with good results with the collections from 48 strokes. In August and September four more meters were covered with the inverted can, but the difficulty in finding the specimens was so great that all results were discarded.

A summary of the inverted cylindrical can data and observation counts for representative collections is given in Table 1. The original data of one of the large series of sweep net collections and one series of observation counts are presented in Table 2 to illustrate variations in collections.

In Table 1, column 2, and Auerbach (1949), Table 2, the number of categories, often representing single species as nearly as could be ascertained in the field, is shown common to both net and cylinder collections. One collection made both with the m² can and the sweep-net on Oct. 15, 1946, on a very cool morning. Five species were found in both can and net catches. The can total was 86% of the net total. Of specimens belonging to these species in the collection of 6-16-47, categories 2, 5, 15, 18, 19a, 30, 32a, and 32b were found in both collections and the can total was 75% of the net total of specimens in these categories.

TABLE 1. Showing relation of sweeping (48 strokes) collections to 1 m² cylinder collections and observation counts.

1	2	3	4	5	6
Dates	Number of categ. same in both coll.	Percent of sweep number of indiv. in cylinder	Dates	Number of categ. same in sweep and counts	Percent of sweep number of indiv. in counts
Sec. I......	Cylinder		Sec. II	Herb Counts—3 observers	
9-20-45...	4	82	9-11-47	18	56
10-15-46...	5	86			
6-16-47...	8	75		Shrub Counts—3 observers	
6-20-47...	6	71	9-11-47	22	52
6-23-47...	7	74	8-26 and		
6-26-47...	8	73	8-31	9	65
	Mean......	76.8%		Mean......	57.7%

TABLE 2. Sec. I shows a typical series of summer sweep net collections such as were compared with the cylinder collections shown in Table I. 1-6, Sparkman-Wetzel in Trelease Woods, and 1-10, Auerbach in Brownfield woods are two series made in rapid succession over different ground; * mean. Sec. II, columns 1-9 are two observer observation counts. Columns 10 and 11 are 3 observer counts.

Sec. I Sparkman-Wetzel 6/16 to 6/27/47	1	2	3	4	5	6	7	8	9	10	11
Total Specimens......	332	426	486	255	323	267	350*	352	–	326	–
Crane Flies..........	9	7	11	4	9	7	–	3	–	3	–
Harvestmen..........	11	38	34	8	18	15	–	16	–	12	–
Spiders..............	20	22	25	18	16	9	–	22	–	42	–
Tree Cricket..........	9	9	8	7	7	13	–	13	–	9	–
Pupoid snails.........	3	5	8	11	2	4	–	14	–	7	–
Anoplitis.............	12	13	20	9	13	18	–	33	–	30	–
Red-eyed flies........	23	35	67	51	59	34	–	0	–	30	–
Nabids...............	3	14	18	2	7	4	–	3	–	3	–
Auerbach 9/16/41											
Total Specimens......	118	139	153	148	103	116	126	100	98	109	121*

Sec. II 8/21(1); 8/25-26(2-9); 9/11(10-11)	OBSERVATION COUNTS										
	1	2	3	4	5	6	7	8	9	10	11
Total Specimens......	28	49	40	20	11	46	63	76	51	77	50
No. less nondescripts..	25	48	39	19	11	41	33	47	47	66	42
Anoplitis.............	5	15	19	3	4	23	13	6	7	29	7
Nabids...............	1	7	3	0	2	0	3	3	1	0	0
Dolicopodid Flies.....	6	4	1	0	1	1	6	5	2	0	5
Brown leafhoppers....	8	6	2	1	0	6	0	1	0	0	3
Mangora sp. spider....	1	1	2	3	1	1	1	3	0	3	1
Total spiders.........	4	6	6	9	2	2	4	5	9	9	12
Tree Crickets.........	0	0	2	0	1	0	0	0	0	1	0

The average percentage of the sweep-net collections represented under the can (of the mutual categories), as shown in column 3 of Table 1, is nearly 77%. A different method of calculating the ratio based on the total numbers of individuals regardless of whether the categories occurred in both collections was tried and found to give nearly the same results. This indicates that a net collection equals the population on approximately 1.25 m². However, the number of sweeps used has not been reduced for the following reasons: (1) The most careful search of litter and herbs under the can will fail to find all specimens. Hence the actual number under the can will be larger than the most careful count indicates. (2) There is evidence from a number of trials that reduction of the number of strokes of the net would not bring a proportionate reduction in the number of specimens caught. As shown in Table 2, there is a large variation in the number of specimens taken in consecutive sweeps over different ground by the same person. Wetzel's smallest collection was 73% of the mean of her six. Auerbach's smallest collection was 81% of the mean of ten collections. There were differences in the uniformity of the vegetation. Wetzel's collections were made in a poorly drained area in a rainy June, when the vegetation probably varied more from place to place than in the average June. Auerbach's collections were made under ideal conditions of vegetation and with immature delicate arthopods at a September minimum on the herbs.

Evidently the efficiency of the net decreases as the number of strokes increases, because of the accumulation of plant material in the net. Accordingly, a reduction in number of strokes does not give a proportionate reduction in the number of specimens. The 48 strokes have been retained for the sweep-net collection size, since it is a standard unit used throughout the study except for the first two years, when 50 strokes were used.

Observation counts compared to sweep-net collections were uniformly lower than were can collections compared with sweep-net collections. This can largely be attributed to the omission in the observation of numbers of individuals hopping and taking to flight, or in flight, which are regularly caught by the sweep-net. These flying individuals must be considered as a part of the population at the time of sampling, regardless of their transcience. A considerable part of the observation deficiency results from failure to see the small animals before they fly or before they fall from the herbs or shrubs to the ground.

The observation count method is primarily valuable in determining the degree of uniformity of species distribution over the herbage. There was close agreement between the numbers of species present in both observation counts and sweep-net collections. In all the work done, only four categories in the observations were not in the net collections; (a) snails, too low to be reached by the net except when the humidity is high; (b) two spider categories, too high in the shrubs to be reached by the net; (c) an accidental species. The fourth category missing in the net collections was a sapromyzid fly of the genus Homoneura (probably *H. incerta*) which declined and disappeared about the middle of the period. One dolichopodid fly (probably *Sympycnus lineatus*) disappeared and another took its place, accounting for other vacancies.

Of the species given special attention, *Dicyphus gracilentus* (see Fig. 13, page 205) was scarce throughout the summer. Only two specimens were taken, one in the test sweeps, and only one in the observation counts. The spider, *Mangora gibberosa*, occurred in all collections, ranging from 3 to 11 individuals, and was seen during all observation counts.

The wedge beetle, *Anoplitis inaequalis*, was present in all collections but was variable in number. The high number in late June (Table 2, Sec. I) suggests an increase due to emergence from the pupal stage. It is obviously not uniformly distributed, as is shown by a range of 26 (3 to 29) in the observation counts and 88 (9 to 97) in the late summer sweeps (Table 5, H). It is relatively sedentary on nettle leaves, i.e., does not move unless definitely stimulated, and thus can be counted fairly accurately. Square-meter areas with very low populations can easily come about through the diversion of heavy rainfall onto particular small spots by branches of large trees. A square meter with only 11 total specimens (Table 2, Sec. II, Col. 5) can hardly be explained otherwise.

This analysis indicates the sweep-net collections include representatives of all the species noted in observation counts except those whose habits put them out of reach of the net at times. Observation count totals for single meters varied sevenfold; sweep totals varied only a little more than twofold at the same season. The variation of catch of *Anoplitis inaequalis* was about the same in both methods when data not in Table 2 are included. The observation counts emphasize the fact that the animals are very definitely not uniformly distributed, even on as nearly uniform vegetation as can be selected by observation. The total numbers of spiders, and of individuals of other species were generally more uniform in the sweeps than in single meter observations, or in the one m^2 cylinder recoveries.

It is necessary to deduct small flying and hopping insects (category 35) which cannot be identified and which frequently may be said to swarm into the observations. For example, 118 minute leafhopper nymphs were taken in a single August-September sweep collection (none in any other collection) and at the same time 30 other minute forms occurred. These are deducted from a total of 376, leaving 228.

The can method of collection used on the herbaceous vegetation obviously cannot be used in checking shrub populations. Here the observation count method was the only one feasible for checking the sweep-net sampling. A wire ring enclosing an area of 0.1 m^2 was used to delimit the observation counts and was held near a branch; the amount of foliage and the kinds and numbers of animals were enumerated. Each of these observations was intended to represent the volume stroked by a sweep net. It is evident that most of the specimens from such a volume are not caught by a net (cf. previous discussion of the sweep net). The relation of sweeps and counts for shrubs was similar to that found for the herbs (Table 1).

The collections from shrubs were almost without exception smaller than the collections from herbs. The totals, May through September, 1943 to 1946, and May through July, 1947, made by the same observer, average almost exactly 40% of the herb collections. For other months of the year, the ratios are more variable than in the months included in the average.

The population of the trees was not studied especially because of a lack of necessary assistance and serious difficulties associated therewith. A typical large tree in the area of study has a trunk circumference of about 1 m at breast height. The trunk is divided into four more or less main branches at the height of about 12 m. The four branches divide again into two or three smaller branches about 4 m from the first division, giving ten or twelve smaller branches which have rough bark for about 3 m. Beyond this point, the barks of many trees are smooth. The rough bark of such a tree has a surface of about 35 m^2, making the bark area about ⅙ of the crown area, i.e., the area covered by the crown when projected onto a plane surface. An occasional small

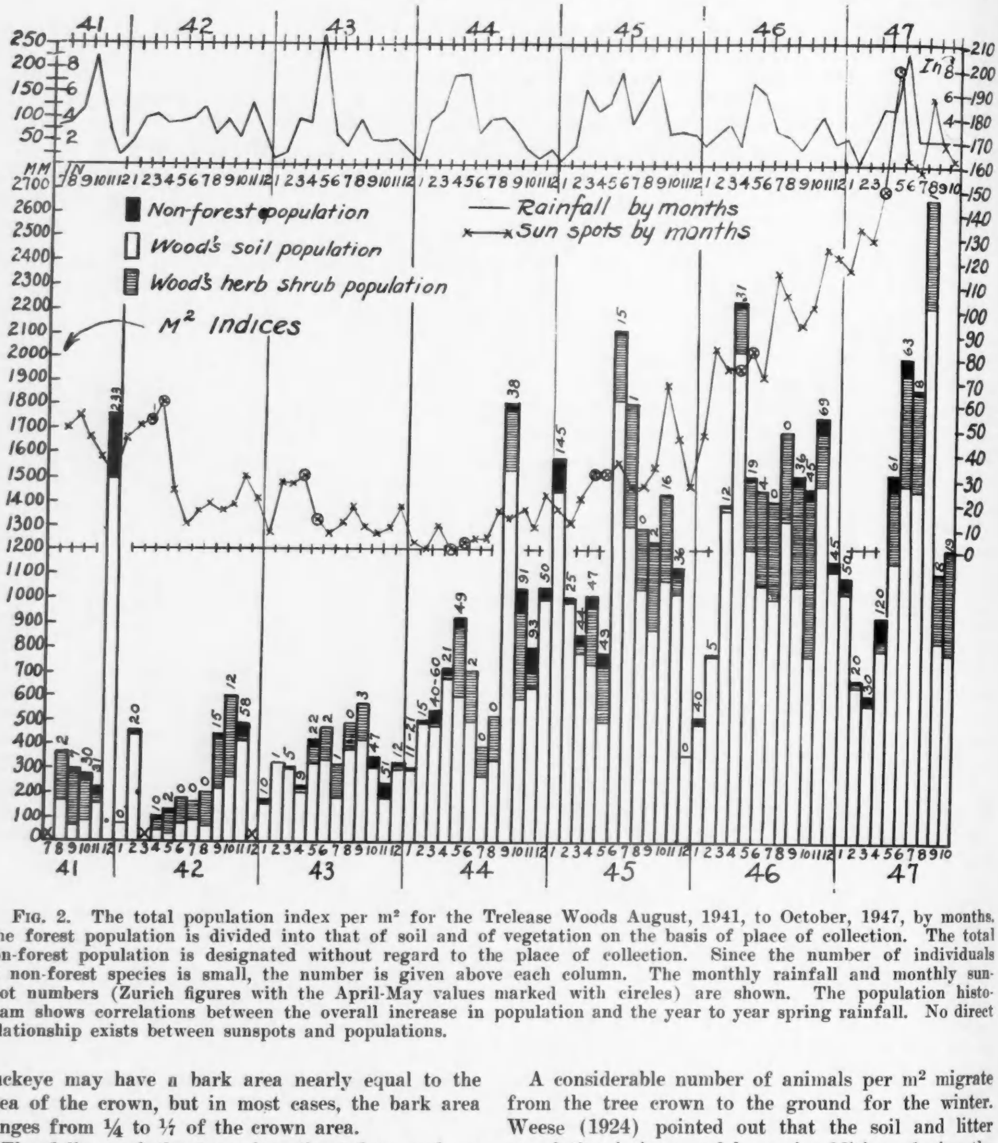

Fig. 2. The total population index per m² for the Trelease Woods August, 1941, to October, 1947, by months. The forest population is divided into that of soil and of vegetation on the basis of place of collection. The total non-forest population is designated without regard to the place of collection. Since the number of individuals of non-forest species is small, the number is given above each column. The monthly rainfall and monthly sunspot numbers (Zurich figures with the April-May values marked with circles) are shown. The population histogram shows correlations between the overall increase in population and the year to year spring rainfall. No direct relationship exists between sunspots and populations.

buckeye may have a bark area nearly equal to the area of the crown, but in most cases, the bark area ranges from ¼ to ⅐ of the crown area.

The foliage of the trees is estimated to make a layer 4-6 m thick over the entire woods. Smith-Davidson (1930) estimated that the leaves and bark of an average maple tree supported a total population of 1,470 insects and spiders per m² of horizontal surface beneath the tree. It is evident that the bark population is large. The area of the tree crown was not given by Smith-Davidson and the understory of seedlings too high to reach with a sweep-net was evidently ignored. The total population for the ground, litter, herb, and shrub strata beneath the tree was found to be 1880. This figure compares favorably with the high records for 1945 in the Trelease Woods.

A considerable number of animals per m² migrate from the tree crown to the ground for the winter. Weese (1924) pointed out that the soil and litter population is increased by such additions during the autumn period. This is very obvious in the case of leafhoppers of the *Erythroneura obliqua* group, which come down from the trees in late autumn. In one case they were caught by sudden cold weather and the bark of maple and basswood trees held many of them until a warm period enabled them to move again. They occur in a very scattered pattern over the forest floor and also in aggregations, notably under basswood seedlings, where in one case an aggregation occurred quite regularly over a period of twenty winters, with numbers estimated as high as 10,000 invidual in some years and about 1,000 in others in an area of 2 m². The Erythroneura

group appears to be the largest contributor to the increase from the trees.

Not all tree inhabitants leave the trees in winter and may suffer heavy mortality as the autumn and winter progresses. Smith-Davidson (1930) lists five species of spiders that are taken in trees only, viz. *Theridion punctiparsum* Em., *T. murarium* Em., *Eustala anastera* Walk., *Araneus curcubitinus* Clerck, and *A. labyrinthus* Htz. Little is known of the bark dwellers, which may include many strictly tree-inhabiting species.

Those insects from the fields increase the number in collections except during a 60 to 90 day period in midsummer (Fig. 2); the June, July, and August numbers are usually insignificant. Usually there is only a small number of individuals of the six species recognized as non-forest still on the herbs and shrubs in June. Some of them may occasionally breed in the woods. This is probably true of the two species of Notoxus which are occasionally taken in midsummer. Furthermore, Blake (1926, 1931) took nymphs of the tarnished plant bugs, *Lygus oblineatus* (Say), in June, 1925. In this year there was a serious April-May drought and temperatures above normal. This is our only record including the work of Weese (1924), Smith-Davidson (1929, 1930), and the current study. Records of non-forest animals after June 15 are probably due to individuals too weak (e.g. chinch bugs) to leave the woods. The non-forest population is only a small part of the total population and does not constitute any important addition except in years when they are extremely abundant (Fig. 2).

Normally, in addition to the tree stratum species, the herb and shrub strata species migrate to the ground for overwintering and altogether they may swell the soil collections as much as 300-400 per square meter for a short time in the autumn of years of high forest populations. This increase is lost sight of as the regular soil inhabitants migrate below the 3 in. (7.5 cm) level marking the lower limit of soil collections in the Trelease Woods. A large segment of the population is not sampled in winter because of vertical migrations in the soil, especially during winters with prolonged cold when the Trelease Woods soil may freeze to a depth of 3 to 4 in. (7.5-10.0 cm). Table 3 shows these apparent vertical migrations in the winter of 1947-48. Jacot (1936), Pearse (1946), and Starling (1944) report large numbers of animals of the kinds we have been censusing below 7.5 cm in the North Carolina deciduous forests.

The normal total forest population shows two peaks, one in early summer and one in late summer; the autumn decline begins in October. In 1947 (Fig. 2), the peaks are obscured by the unusual occurrence of a large number of soil staphylinid beetles (over 1,000) in one of the collections. These two peaks may be ascribed to life history phenomena such as the emergence of new generations (e.g. Figs. 3 4B).

B. COMPUTING POPULATION INDICES

In general terms, the figures used in this paper are *population indices* rather than absolute population numbers. Taking into consideration the large tree population and the omission of groups that cannot be sampled, it is probable that the total indices represent the magnitude of about half of the invertebrate population composed of individuals large enough to be counted readily with the naked eye. Monthly indices are represented by the average numerical values of catches per unit area of all the collections in the month. Annual indices are calculated as the average of monthly indices for a certain number of months. In the case of each species the number of months which best represent the population produced in the reproductive period of the year were used insofar as knowledge permitted.

TABLE 3. Suggesting downward-upward movement of soil animals related to depth of frost. The figures are numbers of individuals per m² based on 0.2 m² sampled each month to a depth of 7.5 cm.

Categories	Depth of Frost			
	Dec. 1.2 cm.	Jan. 2.7 cm.	Feb. 13 cm.	Mar. 0
Total individuals	1670	1120	950	2010
Herb-Shrub spiders	190	160	85	330
Leaf Hoppers	40	0	0	70

An example of the application of the method may be given in the case of Gargaphia, November, 1937, and August, 1938.

November 1937					August 1938				
Date	Ground*	Herbs	Shrubs	Total	Date	Ground*	Herbs	Shrubs	Total
11-1	0	1	0	1	8-1	0	1	0	1
11-8	0	0	0	0	8-9	0	1	4	5
11-15	10	0	0	10	8-16	0	1	26	27
11-22	30	1	0	31	8-22	0	10	9	19
11-30	0	0	0	0	8-29	0	11	25	36
			Gr. Total	42				Gr. Total	88
	Average of 5 collections			8.4		Average of 5 collections			17.6
			10 m²	84				10 m²	176

*The one-tenth meter catch is multiplied in making the records for a m².

In the case of Gargaphia the new generation indicated by the late summer and autumn collections is shown in Fig. 3 by the curve with X's. This line represents the year to year population of the new annual generation with the first maximum in 1938, and is 80% (see p. 190) of the average of the July through October collections. It is the curve that would be used to consider the year to year changes in population. Only the specimens taken from the herbs and shrubs are included in the July through October curve. This is the only case in which the 20% reduction has been made in order to make the figures more readily comparable to the soil collections.

C. EVIDENCE OF ADEQUACY OF SAMPLING FROM LIFE HISTORIES AND RESPONSES

Some of the records are in themselves evidence of

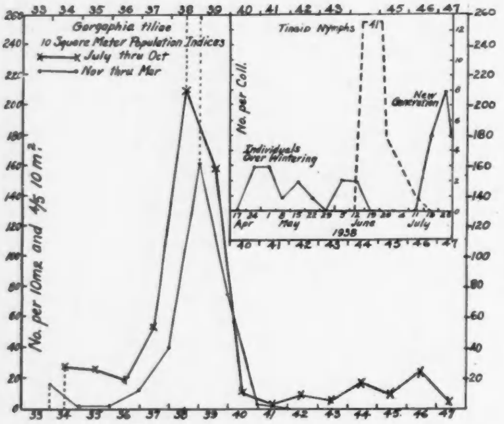

FIG. 3. The life history and seasonal history of populations of *Gargaphia tiliae*, a lace bug of the family Tingidae. The late summer and autumn population is indicated and plotted on the center of the space allotted to each year. This graph is marked by an X. The overwintering November through March population is marked by a dot. When populations were high the overwintering population was smaller than the late summer and autumn total, probably resulting from normal mortality, due largely to predation. After 1941 no overwintering specimens were taken. The insert, individuals per collection (48 sweeps) shows the number of overwintering individuals taken on April and May dates in 1938. This population fell to zero on June 19 and on that day there was a collection of 41 tingid nymphs. These continued to appear until July 11, and were followed by a new generation of adult Gargaphia, the largest collection being only about 1/5 of the largest collection of nymphs and the new generation between two and three times that of the overwintering generation.

the adequacy of the sampling. The analysis of the behavior of populations of *Gargaphia tiliae* (Walsh) was undertaken to bring out an example. In Fig. 3 the lower curve represents the population surviving hibernation. The upper curve represents the average autumn populations after heavy losses due to predators, such as southward-migrating song birds, nabids, reduviids, and spiders.

Conditions under which populations of Gargaphia live naturally lead to an expectancy of a smaller index for the winter population than for the summer. Fig. 3 bears out this expectancy. The decrease in population for the winter amounts to about 25%, as is shown for 1936, 37, and 38. There is evidence of two more tendencies; first, a decrease of nearly 50% in the overwintering population when it starts to decline suggests a physiological weakness, and second, when the population is very small, 0.2 to 0.4 m^2 of soil per month, aggregating 1.0 to 2.0 m^2 during five or six months in the hibernation quarters, is not sufficient to give reliable estimates of population.

However, the behavior of the Gargaphia population, from November, 1937, through March, 1938, from April through July, 1938, and through the winter of 1938-39, can be analyzed. The record per 10 m^2 for the months in hibernation in the winter of 1937-38 is as follows: Nov., 80; Dec., 25; Jan., 40; Feb., 25; Mar., 25; with an average of 39 individuals per 10 m^2 for the five month period (see Fig. 3). The November collections show that the population had nearly all gone into hibernation and only those individuals in the soil were counted; continuing with this same population, specimens taken from the vegetation were the only ones found in the spring (Fig. 3 insert). The 1938 collections showed 3 in the sweeping on April 24, 3 on May 1, 1 on May 8, 2 on May 15, etc. The calculated averages for the month on 10 m^2 are April, 8; May, 14; and June 10—based on the collections on June 5 and 12, with no further record for June. There is a record of 41 tingid nymphs, not identifiable, on June 19, and other much smaller numbers in late July and early August. The first adult *Gargaphia tiliae* were recorded on July 18; the population increased until September 12, when the two sweep collections contained 154 specimens. The average, July through October, was 209 specimens per 10 m^2 or 480 sweeps. Four-fifths of this is the curve x and shows that the overwintering population shrank though the amount is reduced by the method of averaging five or more months.

The hibernating and preceding summer populations are shown in Fig. 3, with the spring, overwintering and the new generations plotted as weekly catches up to July 24. This new generation increased to 154 individuals in 48 sweeps and then the numbers declined as the insects went into hibernation. The collections are shown to be adequate for 1935-41 largely through the separation of the two generations and noting the reduction of population during the winter. From 1941 to 1947 no winter specimens were taken from the soil (Nov.-May, Fig. 3), so the winter curve could not be continued. The insects probably moved to the vegetation quickly in the spring and were missed; more soil collections would have been advantageous.

A different type of evidence for and against the adequacy of the samples is in the data for a fly (*Pseudogriphoneura crevecoeuri* (Coq.)) population in 1937 and 1938 (Fig. 4). Population curves for each year show a period of 5 or 6 weeks between the first mass appearance of adult flies and the beginning of a sharp decline. This is almost the same as the spread of the emergence of the adult codling moths (a south European forest species) caged in screened trees. These adult moths live 3 to 15 days, with an average of 7 days (Glenn 1922). This is a fair average life for most of the hardy insects. Glenn also found (1922, chart 2. p. 270) that a 20° F. drop in the average temperature for three days stopped moth emergence and greatly reduced the transformation of all other stages. Smaller drops in temperature gave roughly proportional results.

As to the size of fly collections in relation to conditions, Fig. 4 shows that there was a large population June 28 to August 16, when a decline had

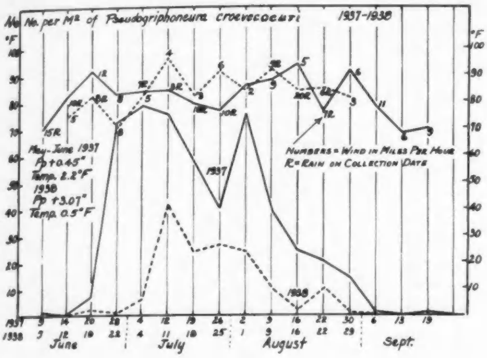

FIG. 4. A. The relation of the collections of *Pseudogriphoneura crevecoeuri* to variations in temperature, wind, and rainfall from collection to collection. Note (a) sharp increase to maximum. (b) Beginning of decline after five or six weeks and responses to weather while population is large and probable inadequate sampling when collections yield less than 10 or 15 specimens. Note sharp increase to a maximum, beginning of decline after five weeks.

evidently begun. After first big lot emergences before June 28, the catch was reduced by wind of nine miles per hour, lowered temperature and rain. Differences between collections totaling less than 10 or 15 individuals are not regarded as reliable, as it is assumed that the insects tend to come to rest in protected situations out of reach of the net.

The total number of flies (Diptera) collected varies in a manner similar to that of Pseudogriphoneura, Figure 5, April, 1937, through October, 1938. In this figure (Aug., 1936 through Oct., 1939) variations in the catch of small brown beetles, Melanophthalma (chiefly *M. distinguenda* Com.), some not identified to species, and probably a few other beetles which resemble Melanophthalma are shown. The catch of the large population, which usually lasts about three weeks, varies with the temperature or wind velocity with an exception, May 30, 1937, which is unexplained. The collection was small while the temperature was high and the wind only nine miles per hour. It is assumed that this is the beginning of the decline as the catches got above an assumed unreliable minimum only on June 20.

The curve of total Diptera is drawn both with and without the phorid. With the phorid fly eliminated, there is a rough agreement between total Diptera and changes in temperature. The phorid flies' emergence is rather explosive, as is shown on July 19, and again on September 13, 1937. Phorid individuals evidently do not survive long enough to give a stable population which would show the response with only weekly collections. The same is true of the autumn populations.

Figs. 4 and 5 indicate that external conditions influence the size of insect collections three ways: (a) lowered temperature and wind above eight miles per hour cause the flies and small beetles to move into positions in which they are not caught; (b) lowered temperature decreases emergence; (c) higher temperature increases activity, which makes the insects accessible to the net; it also increases mortality of older flies, but if the majority in the age classes present June 28, 1947, were dead on July 4, emergence and flight activity probably control the size of the collections considered. If the sampling were inadequate, the response would not be reflected. However, it is a wise procedure to defer net collection when weather is unfavorable on regular dates and to repeat doubtful net collections as soon as weather is more favorable. This practice was followed insofar as possible. Collections on alternate days are desirable in response studies.

As to other species, the sampling of *Epitrix brevis* Sz. and *Baliosus ruber* (Weber) was examined in a manner comparable to the examination of the Diptera. Adequacy was indicated when populations were average and high, inadequacy during the periods of very low population. Figs. 4 and 5 illustrate the adequacy of both population indices and collections. Fig. 4 shows that the collections of Pseudogriphoneura were consistently smaller in 1938 than in 1937. They emerged in mass 14 days later. The 1937 populations came from one in 1936 about 1/16 of its size. The number of collections was reduced to 3 per mo. in 1940 and to 2 per mo. in 1942. The monthly and three monthly means resulting from using the 4-collection method (4) and the two-collection method (2) are as follows:

	June (4)	June (2)	July (4)	July (2)	August (4)	August (2)	Mean 3 mo. (4)	Mean 3 mo. (2)
1936	..	..	6	3	..	..	2	1
1937	20	1	65	67	34	49	40	39
1938	1	1	24	15	9	13	11	10

Both collection frequencies show the variations of the population. The 4 collections in this case lessen the variation slightly. A similar study of the small beetle and total Diptera populations of Fig. 5 indicates similar relations.

The millipeds present the most complicated life histories and general relations of any of the important invertebrates. Fontaria has life histories requiring 2 years; there are seven immature instars (Fig. 6). Starting with 1939, the population was made up largely of adults and instars 5, 6, and 7. The increments of early stages were small in 1939, 1940, and 1941, but fell to almost zero in 1942, indicating that it was the least favorable year for reproduction. Meanwhile the 5th to 7th instars had become adults. There was good reproduction in 1943; the highest rate of the period was in 1944. The rate continued high in 1945, 1946, and 1947. Mortality among the 5th-7th stages must have been high in 1945 since the decrease in these is not followed by an increase in adults. It is evident that the collections were too few in number to make a full analysis of the Fontaria population from the

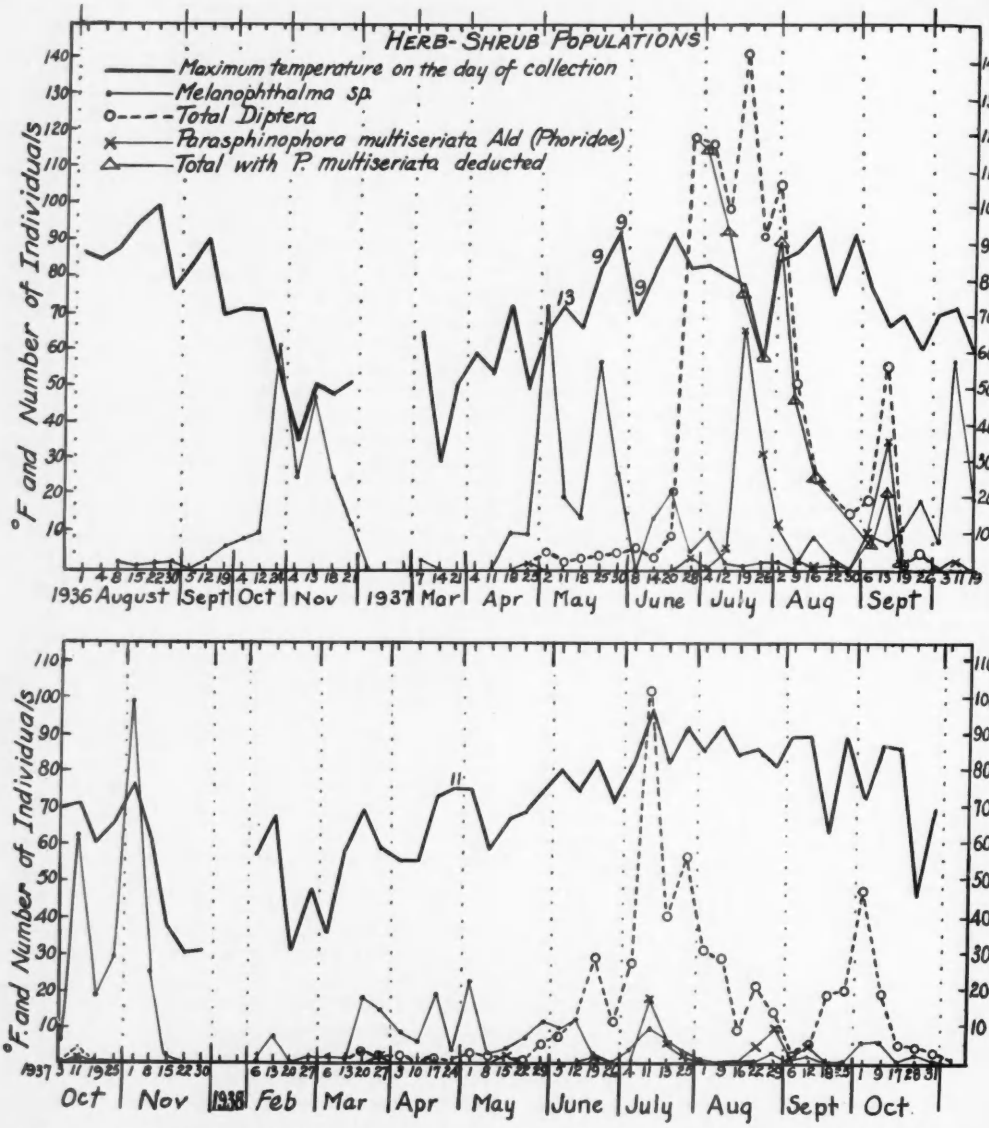

FIG. 5. The figures above the temperature line show the wind velocity on the date indicated. This compares the collection size of a beetle, Melanophthalma, the total Diptera, and the phorid fly, *Parasphinophora multiseriata* Ald. with temperature and wind velocity on the dates of collection. Note large to total fly populations lasting six weeks, large beetle populations lasting three to five weeks, and short-lived populations of the phorid and of September Diptera which rise and decline too rapidly to show responses with weekly collections.

standpoint of life history stages, but sufficient to show favorable and unfavorable years.

The variability of the size of samples is striking in the case of the wedge beetle, *Anoplitis inaequalis* (Web.), especially in the autumn. Figure 7 (see Table 4). It has a decided preference for wood nettle, though it is reported from a great variety of plants. Its larval and pupal stages are not known, but the larvae may be expected to feed on the same plants as the adults. When present in average numbers, Anoplitis occurs quite regularly in collections from the beginning of May through the first half of November.

Overwintering adults of Anoplitis are referred to as old generation, which emerge from hibernation about May 1. There are records of mating in May. Although the larvae have not been identified, there is evidence from the population that freshly emerged

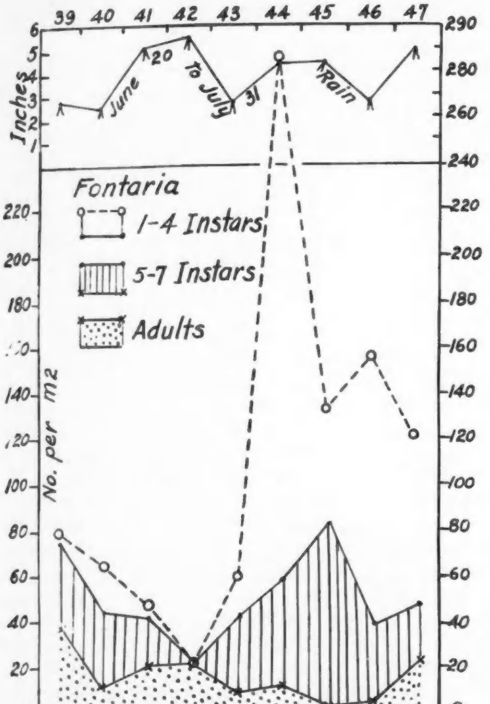

FIG. 6. The population of Fontaria is divided into three groups: 1st to 4th instars, 5th to 7th instars, and adults. The 1944 increase was due to the 1st to 4th instars, which made up 230 of the 288 total. Their place was taken by 5th to 7th instars in 1945. Mortality of 5th to 7th instars probably prevented an increase in adults in 1946.

individuals usually begin to appear between June 30 and July 15, while some individuals of the old generation are still alive. The new generation goes into hibernation in late October and early November, but individuals are taken during the winter only when populations are very large and winter temperatures high. The mean of maxima temperatures for January, 1946, when specimens were taken was 48° F.; maximum of the month was 57° F. Some specimens of Anoplitis may also be caught on the way into the soil because of a collection falling on a particular day. They evidently burrow into the soil without delay upon leaving the plants, as is the habit of some other chrysomellids.

Figure 7 shows the several methods of plotting populations of Anoplitis and Dictyna. Section I shows graphs (a) of the percent of collections with no specimens. These graphs are the reverses of the usual population curve. Graph a, Anoplitis, is to be compared with d, of Sec. III, Figure 7 and Graph a, Dictyna, with Figure 14.

An inspection of sampling records suggests the largest collection in any year and is usually a good index of total population. This largest collection is

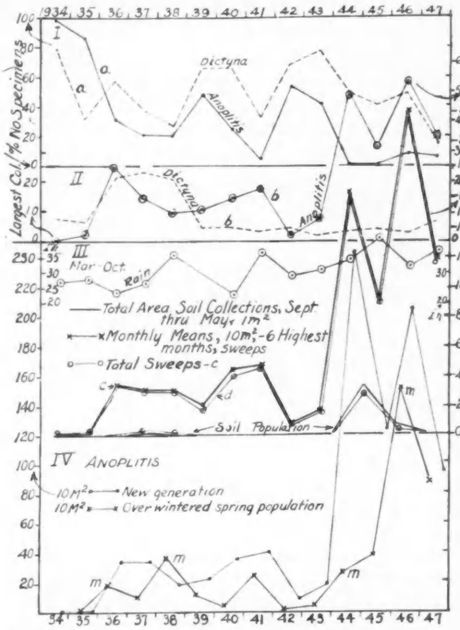

FIG. 7. The relation of population indices of Anoplitis and Dictyna to annual variations in collections made April through October: (a) (Section I) Percent of collections with no specimens. (b) (Section II) Largest number of specimens in any collection. Graphs a and b for Anoplitis are to be compared with c (Section III) which represents the population indices (individuals per 10 m²) for essentially the same period; (a) Anoplitis is the reverse of c, and b is nearly parallel with c. a and b Dictyna must be compared with Fig. 14 (Dictyna).

Section III, c shows the average number of individuals per 10 sweeps per month, averaged for the months used, in comparison with the (d) total number of individuals in the total number of sweeps for the year increased to numbers per 10 sweeps. Winter soil collections treated in the same manner are shown.

Section IV is concerned with winter survival. The autumn population is compared with the overwintering population shown in the following spring. There is quite generally a winter loss. The overwintering population appears to exceed the preceding active population at the points marked M probably due to an insufficient number of samples.

shown for Anoplitis and Dictyna in Figure 7, Section II. The Anoplitis graph is nearly parallel with the population graph, Section III, d. The Dictyna graph is similar to the population curve as shown in Figure 14. These facts (absence of specimens and the largest collections) indicate the validity of the population annual indices.

The total specimens divided by the total area from which they were collected gives a correct number per unit area. However, the indices were not calculated in this way. The monthly populations used in deriving indices were averages of numbers of specimens from a variable number of collections (1 to 5) per month. The means of these monthly averages

for several months were used as annual indices. The question has been raised as to the difference between the results of this method and the total area method.

Figure 7, Section III, c and d, shows the graphs derived from both methods. The graph of number of sweeps differs only very slightly from the monthly average graph, being slightly higher when the number of specimens is very small and slightly lower when the number of specimens is medium or large, but the relative results are essentially the same. The same is true of the winter soil collections where total areas are used to compare with the results of monthly averages per unit area. The data compared represent sweeps or area considered separately. The monthly averages give flexibility in selecting the period giving best representation of the population from year to year. Monthly averages selected from Figure 4 would naturally be the means of July and August. The total specimens from the total sweeps would not mean very much because of a spread of scattered individuals beyond the limits of the graph as shown.

The graphs, in Section IV of Figure 7, show that overwintering populations appear larger than the population of the autumn preceding in 1936, 1938, 1944, and 1946, although there is no reason to assume that there would be no mortality. The Anoplitis population index for the six highest months agrees very well with year to year changes in the autumn generation.

The fact that the autumn collections of Anoplitis were much more variable than those of early summer may be an outgrowth of the decline in general vigor of its wood nettle food plants in areas with heavy root competition or low soil moisture. Rice noted in the 1934 drought that the nettles were lush only in low spots in June and in poor condition generally later in the season. They were almost absent from a well-drained woodland in 1933 and 1934 when the Anoplitis population fell to an extremely low point. It is probable that survivors on low moist ground, where collections were not made, accounted for the differences in number between autumn and overwintering individuals in 1936 and 1938. This assumption can be checked in the next dry period.

Table 3, showing monthly average populations of Anoplitis from 1936 to 1947, was prepared by using a late July date as the average beginning of the new generation. A variation of about 10 days earlier occurs in warm, moist years. In 1938, July had a larger number (42) than August (27). The discrepancy could not be corrected by shifting to an earlier date on account of peculiarities of weather and collection dates and catches. The figures for the year 1941 were omitted from the mean because of a missing record. There is usually a maximum of overwintering individuals of Anoplitis in May or June and a maximum for the new generation in August or September. There is a low population at some time between June 30 and July 15. Table 3 further shows that the largest numbers in monthly collections fall quite uniformly in August and September. The statistically obtained monthly percentages of the season's total herb population of Anoplitis (1936-1947), to be expected when the separation of generations is ignored and figures corrected for trend, are 26.8 for August and 29.4 for September, which agree fairly well with the highest numbers in monthly collections. The six highest months, usually May through October, include both overwintering and new generation specimens. Twice when there was a sharp decline in population the largest number fell in May, indicating conditions unfavorable to reproduction in that spring reproductive period, and once in October, suggesting preceding unfavorable overwintering conditions and fair reproduction during the preceding spring and summer.

TABLE 4. Monthly averages of numbers of individuals of Anoplitis per 10 m².

Mo. End	'36	'37	'38	'39	'40	('41)	'42	'43	'44	'45	'46	'47	Mean
						OLD GENERATION							
5/15....	30	2	32	0	10	(40)	0	0	10	30	125	0	21.7
6/15....	27	22	42	14	5	(10)	0	10	40	50	190	145	49.2
7/15....	4	12	42	12	0	(30)	10	5	30	35	155	120	46.8
						NEW GENERATION							
8/15....	80	47	27	22	10	(X)	10	5	180	105	370	200	96.0
9/15....	45	71	24	67	90	(77)	15	27	420	130	225	480	144.9
10/15....	23	25	30	6	50	(67)	10	40	280	170	225	180	94.2
11/15....	0	0	0	0	0	(12)	3	0	10	95	5	25	12.5

D. EVIDENCE OF ADEQUACY OF SAMPLING FROM STATISTICS

The variation in the number of Anoplitis taken in collections by the same person in rapid sequence (Table 2, 1-6) led to further investigation of that species. Table 5 shows results of an analysis including the most variable data as shown in the 4th item with a range of 88.

The range in the total population, also shown in Table 5, could have been greatly reduced by subtracting categories 33, 34, and 35, as was done in Section II of Table 2. The categories range from 1 to 90 specimens per summer sweep collection. They are taken mainly on the wing and are identifiable to order with difficulty, almost never to family. The deduction of the categories would have reduced the range in item 2, Table 5 from 231 to 175. The deduction reduced the range for observation counts from 66 to 55.

The probability of making a bad collection in the small number feasibly made was considered. The 95% confidence limits were calculated for four sets of net collections and one set of one m² observation counts of Anoplitis. The limits of collection size of 19 out of 20 collections is shown by the 95% confidence limits.

The collections of Anoplitis shown in Table 2 together, with the regular collections of 1947, total 36 items. The coefficient of variation (s/mean x 100) is 96. For the 48 collections of July, August, and September of 1936 through 1939 the coefficient is 50. For the same period that of *Dictyna foliacea* is

TABLE 5. Showing the 95% confidence limits (95% of the extremes will fall between the figure for number of individuals in a collection, Table 2). W, Sparkman-Wetzel, June, 1947; H, Hanson, September, 1947.

See Table 2	Number of Items	Range	Mean	Standard Deviation	95 Percent Confidence Limits for collection
Net Collections					
Anoplitis W	7	24	19.43	8.36	16.80 to 22.08
Total population W	8	231	345.87	72.18	326.69 to 365.05
Total spiders W	8	33	21.75	8.90	19.39 to 24.11
Anoplitis H	7	88	49.14	35.08	13.40 to 84.90
Observation Counts					
Total population	11	66	40.82	17.31	37.63 to 44.01
Anoplitis	11	26	11.91	8.65	10.39 to 13.43
Dolichopodid flies	11	6	2.82	2.41	1.96 to 3.68
Brown leaf hoppers	11	8	2.45	2.91	1.33 to 3.57
Mangora gibberosa	11	3	1.55	1.03	1.05 to 2.05
Total spiders	11	10	6.18	3.22	5.40 to 6.96

119. In 1946, Dictyna was not abundant enough to make calculations feasible. Anoplitis is accordingly a species suitable for sustained population analyses over a long period of time.

As to other species and categories, Table 5 shows the 95% confidence limits for the total herbs population index and for the total herb spider index, as indicated by 48 sweeps. The totals for the shrubs vary in a comparable manner. The total of herb-shrub spiders is quite stable and constitutes one of the best populations for study. The observation counts of several groups are included also in Table 5.

The total soil collections of forest species in general are more variable from collection to collection than the collection from Anoplitis sweeps. This is due to downward migration from the foliage in the autumn and migration up and down with temperature changes during the winter (Weese 1924). However, numbers were occasionally secured which were relatively uniform over the four collections when made in one month. The non-forest total was most variable, both from collection to collection and from year to year. There may have been variations in the thoroughness with which the soil was searched, but excellent operators did the work from May, 1935, through the rise to the 1938 maximum and the decline which followed. The smaller number of collections may have exaggerated the low of 1942, but the low still persisted in 1943, as indicated by the work of an excellent observer, who continued through June, 1947 (see Fig. 2 and Kanatzar 1936).

It was not possible to identify the vast majority of specimens from week to week, and all the collections were stored from the summer of 1939 through the summer of 1943. The stored material amounted to about 16,000 specimens when week to week identification began again. Some of the collections were lost, leaving no collections for November and December, 1940, March and July, 1941, March and December, 1942. In January, 1943, the policy of a double soil collection in December, January, and February was established, with two collections per month in nine months of the year. In 1947 (July 15), two sets of sweeps with each open season collection were instituted as an outcome of the investigation of sampling. It had been necessary to keep the work within about 20 hours per week, to be done mainly by an assistant. In addition to routine collections, the monthly and yearly totals must be kept up to date, and specimens sent for identification, etc.

4. DISCUSSION AND SUMMARY OF METHODS, CHECKS, AND APPLICATIONS

a. The 48 sweep-net strokes, originally found to yield the population equivalent of one m^2 in grassland, yields approximately the population of 1.25 meters of full height herbs (Table 1). When the herbs are low, the catch is judged to be less, probably equivalent to the populations in about 1 m^2. A correction reducing sweeps to ⅘ the catch is made only when sweeps and ground collections are compared. The 1.25 figure used during the growing season was allowed to stand to compensate in part for the population of the tree and high shrub foliage populations which come to the ground for the winter and make the ground collections higher than otherwise.

b. The inverted cylinder method of checking herb sweep-net catches is valid when all specimens of several species can be recovered after killing. Recovery depends on the color and size of the specimen and the conditions of the soil and litter. The soil must be moist and without cracks.

c. Approximately half of the species with considerable populations are slow moving and the majority (estimated as 60-80%) of them may be counted on and near the vegetation of definite areas by *three* observers. In order to secure representatives of all species taken by a sweep-net, two square meter counts were necessary by the observation method.

d. Shrub counts followed the same relations as the herb counts.

e. The entire quantitative estimation must be based upon meticulous recovery of all specimens from the collections. A careful examination of both sides of every leaf, before the foliage wilts, is essential to recovery of all swept specimens. Other methods may yield as much as 15-20% less than the correct total. Berlese funnels do not recover snails; the Morris soil washer destroys delicate specimens.

f. The observation count method can be used to determine the degree of uniformity of distribution (Table 2, Sec. II, p. 23b). For example Anoplitis is qualitatively but not quantitatively uniformly distributed. Total spiders are nearest to being quantitatively uniform in distribution as the range is only 10% of the total specimens taken. The other categories considered have a range equaling 14 to 20% of the total specimens. All are probably qualitatively but not quantitatively uniformly distributed. At least two 48-stroke sweeps and two 0.1 m^2 soil collections per month are necessary to approach quantitative uniformity; many more collections would improve the results.

g. The animals abundant enough to be used in this

study are essentially qualitatively uniform in distribution down to about two 0.1 m^2 collections in the soil and 20 to 24 strokes of the net in the herbs and shrubs on fairly well drained ground. If, however, individuals of abundant species avoid low, moist spots, as the population shrinks or moisture increases, the sparsely occupied unfavorable areas will increase in size until it requires a sample of 1 to 2 m^2 to secure a specimen of some common species from the soil and three or four 48-stroke collections to get an individual of every abundant species from the vegetation.

h. The population indices are usually obtained by averaging the number of specimens collected per unit area, first, for each month and, second, for the series of months which has the largest population from year to year. Consideration is given to the life cycles whenever known.

i. The population index curve is usually closely approximated by the curve of the largest number of specimens in any collection in the period used in computing the population index. In the case of single species, the curve of the percentage of collections with no specimens is often the inverse of the population curve.

j. In utilizing the data of any species or category, the following criteria have been largely satisfied:

(1) The size of collections varied with weather conditions at the time.

(2) In the case of species with overwintering adults the number of the overwintering generation specimens was smaller in the spring than in the autumn.

(3) The range of the 95% confidence limits does not exceed 20% of the maximum.

(4) In terms of annual estimated total populations of any species or group of species, the highest population is at least three times as large as the lowest population (10 to 100 times is frequent).

IV. RELATIONS OF INVERTEBRATE POPULATIONS, WEATHER CONDITIONS AND SOLAR PHENOMENA

1. General Conditions Before and During Early Years of the Study

The study began in 1933, which was about the mid-date of the dry period of 1930-1936. During this period, the annual rainfall averaged approximately 3 in. below normal with 1934 and 1936 lowest (−4.80 and −6.33 respectively), and 1931, 0.95 above normal. The temperature during these seven years averaged 1.8° F. above normal with 1931, 1933, and 1934 highest.

2. The Use of Weather and Solar Phenomena in the Analysis of Populations

The solar phenomena problems are discussed in another paper (Shelford 1951). Here the general plan for suggesting correlations of animal populations with climatic conditions consists of the presentation of the population curves adjacent to curves of climatic conditions. Analysis of populations with reference to life histories is illustrated in Figs. 3, 4, 5, 6, and 7. Weather and other environmental data are so far as possible selected with reference to the sensitive periods in life cycles. The reproductive period is usually most sensitive.

In comparing the physiological life histories of the organisms with the progress of the seasons and the seasonal weather variations the season of greatest sensitivity for invertebrates is March through October. It may be advantageously subdivided into two seasons, viz., (1) spring, March through June, and (2) summer-autumn, July through October (Figs. 8 and 11). In some cases March and April averages are important, in others April alone. Any combination of months may prove important. Still more valuable is the breaking down of the weather data into short periods of 10 days or 15 days or of periods suggested by known life histories. The condition of the vegetation is important. Rice (1946) observed that in 1934 the herbs had all died down by June because of lack of rain and high temperature. She stated that the pawpaw, ash, and many other forest trees, shrubs, etc., were nearly defoliated by August and that several trees died. Rice was of the opinion that the quantity of leaves in 1934 was less than in 1933. She referred to the canopy as nearly normal in September and October, 1933, and implied the same for 1935. There appear to be no scientific measurements of canopy density but there is a good basic knowledge supporting Rice's view.

During the 1937-39 high forest animal population, the summer rainfall averaged more than 29 inches. The 1937 and 1938 per cent possible sunshine and relative humidity was high. The March-October sunshine in 1938 was highest of the 14 years except 1947, which was slightly higher (see Figs. 12, 13 and 14). If the trees reacted with added growth much more light would be excluded from the low vegetation and the forest floor than in years with less rain and sunshine. In general terms the increase in non-forest forms came in a period of low rainfall and the increase in forest forms in a period of high rainfall. The declines occurred when the conditions were reversed. However, an extreme low of both forest and non-forest populations was in 1942 (see Fig. 4, Shelford 1951). No reason from the standpoint of weather is evident and some influence of solar radiation is probable.

Rough criteria as to conditions favoring large populations of forest animal species were established through the study of weather conditions in years in which increases occurred. They are:

Rainfall in the last 10 days of March not less than 0.25 in. and the total for the last 10 days of March and the first 10 days of April not less than 2.50 in. or more than 5.00 in. and a mean April temperature of 50° F. or above. Total April rainfall not less than 5 in. and total May-June not less than 8.00 in. or more than 13 in. A 10-day period in May or early June with not less

than 0.25 in. rainfall or more than 0.75 in. appears to be beneficial but it is essential that dry periods be short.

The late summer conditions such as long dry periods reduce the population index of the year in which they occur relatively little but have important effects on the breeding population of the following year. Fig. 9 illustrates the monthly limits of years of increase. Fig. 10 shows the various types of dry periods and lengths of dry periods which are more detrimental to some species than to others, and Fig. 11, month and half month climographs of favorable and unfavorable years.

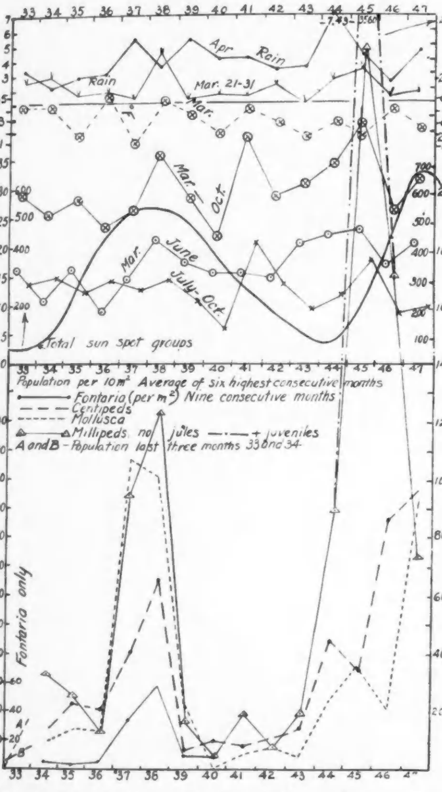

FIG. 8. Shows the population indices of the soil and litter-inhabiting forest species. There was a general high population in 1937 and 1938 and again in 1944, 1945, and 1947. There was a general decrease in 1946 accompanying low March 21-31 and April rainfall; different groups reacted differently. The distribution of milliped populations is due to a two-year life span, a second brood in some species, and an enormous reproduction in 1945. The 1946 decline resulted from the death of individuals which were young in 1945, accompanied by a low rate of reproduction in 1946. The reduction in 1947 resulted in part from death from old age. The Fontaria population is shown from 1934 through 1940. The later history is shown in detail in Fig. 6. The short graph marked A indicates that the molluscan population was higher in the last three months of 1934 than in the same period of 1933. The graph marked B indicates the difference in centipede population in the same period of 1933 and 1934. The irregularities consist of a decline in centipedes in 1945 and an increase in 1946.

3. POPULATIONS OF SPECIES AND GROUPS OF SPECIES

A. SOIL AND LITTER INHABITING SPECIES

Milliped, centiped and some mollusk populations have been considered as chiefly soil and litter inhabiting species in the aggregate and it is these which are discussed. Some trends toward correlation of populations with certain weather and solar phenomena are evident; in other cases little or no correlation can be observed with the methods of analysis and information available. An attempt to point out probable correlations between populations and these phenomena will be made in the following paragraphs. It should be understood that these are based upon a limited number of observations and that, except for a relatively few species of millipeds, there has been little detailed study of breeding characteristics and other life history events susceptible of scientific description. Close observation and many years of records are necessary to establish with certainty the correlations suggested here and elsewhere.

In general, the soil and litter species show a fair degree of correlation between population size and amount of rainfall during their reproductive period. Increases in these populations seem to be favored by moderately high spring rainfall, although population

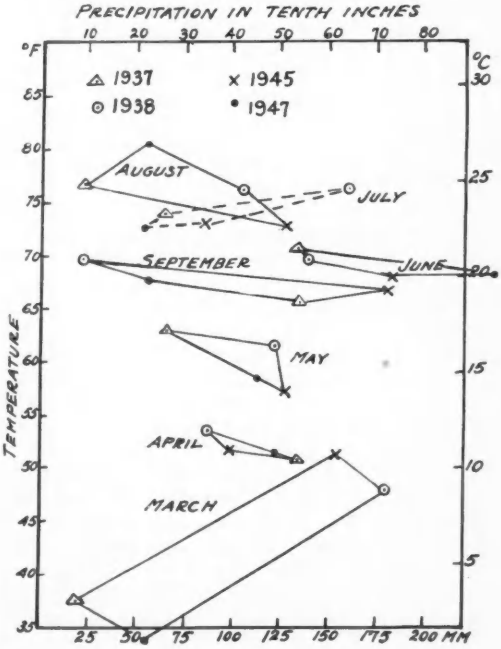

FIG. 9. Shows the limits of temperature and rainfall for the years in which the forest population remained high. April and May fell within the lowest limits or were subject to the least variation from year to year and are considered to be the most important months. (See Johnson 1927.)

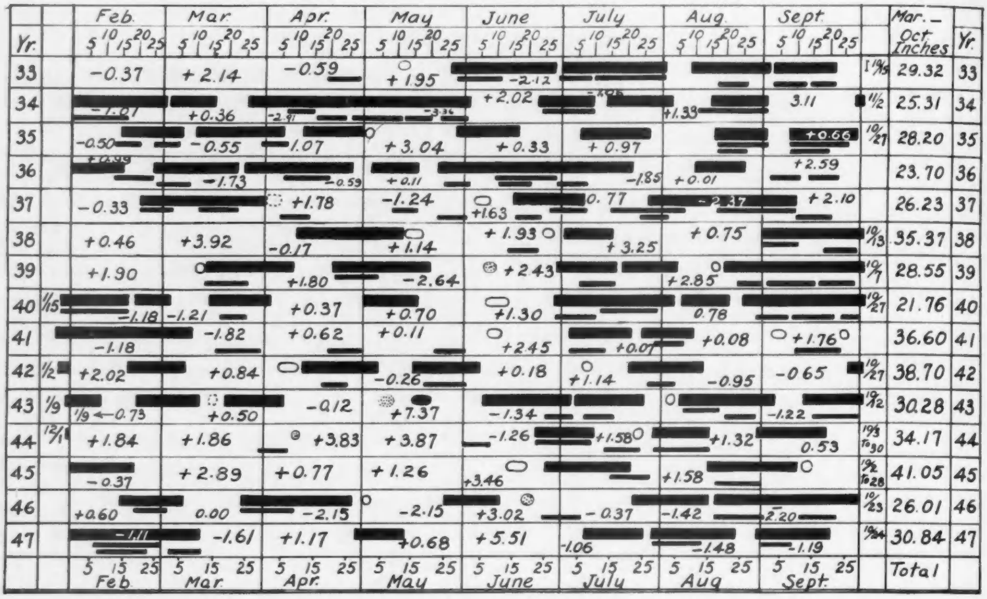

FIG. 10. Shows the drought periods of February through October, 1933 through 1947. The wide black bar indicates periods of more than 14 days with less than 1 in. or 25 mm of precipitation. The narrow black bars are placed at two different levels. The upper one represents 8 or more days with less than 1/10 in. or 2.5 mm of rain. Those on the lower level indicate 8 or more days with less than 1/100 in. or 0.25 mm of rain. The solid black ellipses indicate 5 or more inches of rain within 6 days or less. The stippled ellipses indicate 3.5 or more inches of rain in 6 days or less. The open ellipses indicate 2.5 in. or more or rain in 6 days or less. The broken ellipses indicate 2 or more inches of rain in 5 days or less. Opposite the line representing each year is the total rainfall for March through October. The dates at the ends of the lines at the left indicate the beginning of the drought indicated, and at the right, the end. The average for February through October at the Urbana Weather Station is 27.12 in. The figures such as —1.42 or +1.58 are the deviation from the normal for the month.

The heavy black bars and ellipses representing periods of drought or heavy rains were carefully compiled from weather records and are complete. The narrow bars on the lowest level do not show all the dry periods of the magnitude which they represent. On the lower level, only the periods thought to be significant are shown, since the effects of short period droughts on a forest previously saturated by rain are of little consequence. Similarly, some records are omitted from the middle level.

sizes are rarely a function of a single variable. Figure 8 shows curves of the annual population indices of these groups presented adjacent to curves of selected weather data. The number of sunspot groups for the entire period of the study are added because of their relation to solar radiation. The spring (March-June; March 21 to 31 and April) rainfall in the years 1937, 1938, 1944, and 1947 was high and all litter populations increased. A late April-May drought (Fig. 10) reduced 1939 populations. In 1940 both spring rainfall and population were relatively low but the preceding droughts were probably unimportant. The centipede declined in 1945 with the high March-June rainfall but had increased with considerably less rain in the earlier years, which suggests that there can be too much rain, although the totals of mollusks show the direct relationship. Similarly in 1946 the lower rainfall is correlated with lower mollusk and total milliped populations but not with the centipede populations. Minor variations in records for the periods of very low populations are probably not significant. Sampling frequency and area covered may not be adequate.

The millipeds are typical forest species and have been followed in some detail. They present complex life histories, at least in some species, and serve to illustrate some of the complications which may arise in analyses of populations. Hanson (1948) found the most abundant species to be *Pseudopolydesmus serratus* (Say). Its population is made up of two life history races, one of which breeds in late March and early April and the other in July. Hanson (1948) has analyzed the numbers and shifting of the Pseudopolydesmus instars in the population in a manner shown for Fontaria in Fig. 6, but the Pseudopolydesmus population is complicated by the presence of the two life history races and the probability that at least a significant portion of the adult population lives into the second year. He has suggested that a moderate amount of rainfall in the late March-early April reproductive period is essential for a large population of most millipeds and that drought periods in this period, and to a lesser extent at other times, exert a detrimental effect.

A comparison of the data as presented in Figs. 8 and 10, based primarily upon Hanson's suggested

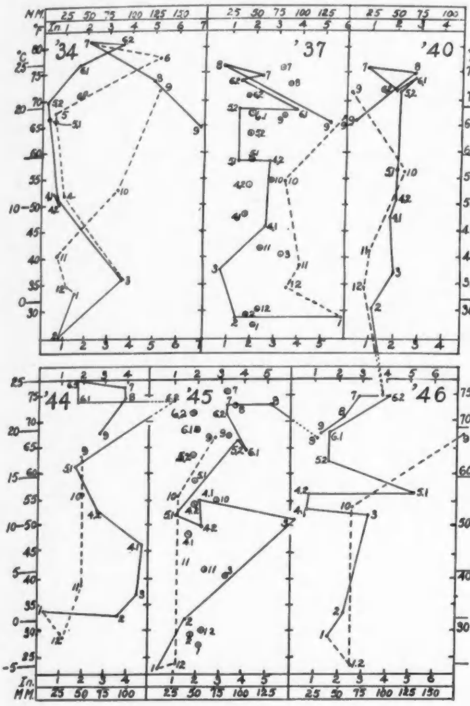

FIG. 11. Shows the climographs of the years 1934, 1937, 1940, 1944, 1945, and 1946 at the Urbana Weather Station with the months of April, May, and June divided in half. The diagrams begin with the September of the year preceding. This portion of the diagram is indicated by a broken line. The diagrams end with September, which when successive years are shown, connects them as a series. The normal or average for each month and the half-months is indicated by a detached round dot accompanied by suitable figures for 1937 and 1945. The numbers indicating the half-months are marked sub 1 for the first half and sub 2 for the second half. In 1934 the regular climograph is indicated for the period of April, May and June by a broken line. Compare 1934 and 1944 in relation to non-forest maxima (see Fig. 18) and 1937 and 1945 in relation to large increases in forest populations (see Fig. 18). 1940 is a year of low temperatures and 1946 was characterized by declines in forest populations.

relation between the population of millipeds and rainfall indicates that the extended drought lasting from July to October in 1946 probably reduced this late summer breeding to a minimum and also destroyed some of the young stages of the spring broods. The reduction would cause the population to shrink in 1947. In addition, 1947 had unfavorable spring conditions with a February-March drought and below normal March rainfall which would further reduce the population of the soil breeding millipeds, causing the 1946 decline to continue into 1947.

In the case of Fontaria (Fig. 6), a single graph is not satisfactory because of marked differences in the distribution of the 5th to 7th instars and adults. Hanson (1948) examined the preserved collection of Fontaria, 1939-1948, and recorded the 1st to 4th instars together as one category and the 5th to 7th instars as another. From 1933 through 1939 and later, the adults and occasional immature specimens later than the 5th instar, probably mainly 7th, were recorded. Rice (1946) found them swarming over the ground on July 17, 1934, and on June 28, 1935, and found eggs on the 1935 date. Ostendorf (1939) stated that copulation of the Trelease Woods species takes place in May. Morse (1906) indicated that the egg laying of *Fontaria indianae* Boll. takes place in early summer and the eggs remain over winter and hatch in the spring, and adults and various stages occur together all summer. Further information is needed to clarify Fontaria life histories. However, the egg-laying evidently falls in a dry period in the latter part of June and early part of July (Fig. 10). Temperatures at or slightly below normal seem favorable to the development of milliped populations (see Fig. 11, '37 and '45), and at least some of the low populations have come when temperatures were high (Fig. 8; see Fig. 15, p. 208). There is no evidence that temperature relations are critical.

There is a difference between the behavior of the mollusk population and that of the millipeds. The study began during and following a severe drought which started in the early spring of 1934 and was only partially relieved by heavy rains in May 1935. The collections in 1934 were practically nil, and notably lower than collections of the combined millipeds and combined centipedes. This was probably due in part to the inactivity of the snails in soil cracks, etc., on account of lack of moisture. Very little is known about the early stages of the snails and slugs of Trelease Woods, beyond the fact that eggs occur from April to early June. The population of these animals in 1934 was smaller than that of the milliped. It increased in 1935 and remained stationary in 1936 while the milliped population declined from 1934 through 1936. The different responses of the two groups is ascribable to relation of the occurrence of dry periods to the sensitive periods of the animals which come at different times in the two groups.

The shelled mollusks have an advantage over the millipeds in that they are able to close their shells with an epiphragm of dried secretions and withstand droughts. This process may have saved the population during the severe drought of 1934. The centipede population behave much as the mollusks did in 1935 and 1936. However, they are not known to have any means of protection unless their thin bodies enable them to penetrate deeper into the soil than the millipeds do. In 1942 to 1946 they behaved as the mollusks did in 1943 to 1947. There was a low population of centipedes in 1945 and a low population of mollusks in 1946, but the only explanation that can be offered is again a difference in the time of sensitive periods in the life history cycle.

B. MOLLUSCAN SPECIES

The molluscan species which contribute to total

population are considered separately. Figure 12 shows the behavior of the populations of 9 species; 2 are combined, making eight groups, viz., *Succinea avara* Say, *Vertigo tridentata* Wolf combined with *Collumella edentula* (Drap.) since the young of these two cannot be distinguished, *Hawaiia minuscula* (Binn.), *Haplotrema concavum* (Say), *Carychium exile* H. C. Lea, *Retinella indentata* (Say), *Mesodon thyroidus* (Say), and *Deroceras gracile* Raf. In addition, a few individuals of *Deroceras agreste* (L.) are sometimes included with the last (see Zetek, 1918).

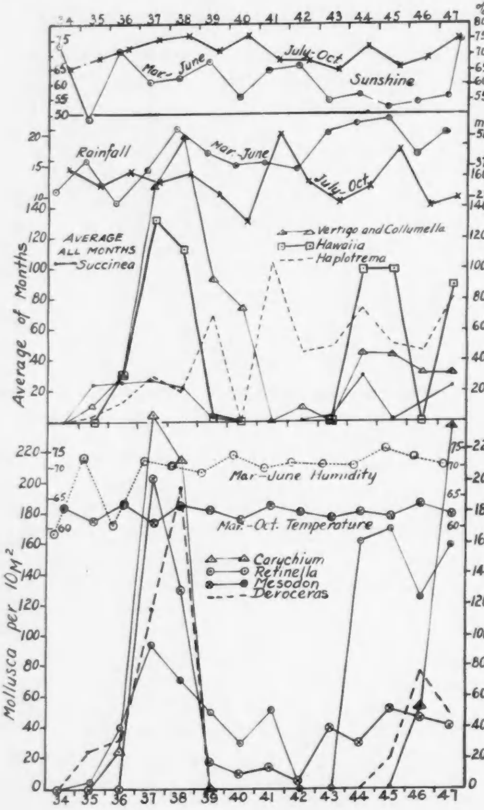

FIG. 12. Shows the fluctuations of populations in eight categories of snails representing nine species. The sunshine, rainfall, humidity, and temperature for the growing seasons are indicated. Most increases are associated with increases in March-June rainfall.

With the exception of Haplotrema and Succinea the populations of the seven species conform to the general trend of the molluscan total in spite of the fact that juveniles were not identified. Figures 10 and 11—'40, indicate that 1940 was the driest year of the 14, particularly in the summer, and also presented the greatest summer and winter extremes. Every species declined or had small populations.

Among the regularly behaving species, knowledge permits discussion of only *Mesodon thyroidus*. This species deposits eggs from May 1 through the middle of August, with the maximum in June. Fertilization takes places principally in the preceding fall (Foster 1937; Van Cleave & Foster 1937; Ingram 1941, 1944). The years 1939, 1940, and 1941, were probably unfavorable to their general activity in autumn. Mr. Glenn R. Webb states that the shell of *M. thyroidus* is thin and it is the first of several species to die of desiccation. The year 1943 might appear unfavorable to this mollusk on account of droughts in both spring and late summer and autumn (Fig. 10); however, as there was an increase in the population of this snail, the drenching rains and excess rainfall of May were probably sufficiently stimulating to reproduction to offset the disadvantages of the droughts. *M. thyroidus* is favored by flood-plain conditions and flourishes under short period spring flooding. However, it is not possible to suggest explanations of the minor changes in numbers, 1939-47 since the sampling is not sufficiently reliable. We are, however, justified in recognizing the 1935-36 low population, the 1937-38 high population which is at least 100 times the earlier minimum, the 1940-42 low population and the 1943-47 high population which averages approximately four times the 1940-42 low average. Autumn droughts may have helped prevent the population of 1943-1947 from reaching the 1937 high point.

Haplotrema is said to feed principally on *Mesodon thyroidus*. There is a suggestion of a predator-prey relation in which Mesodon was reduced and Haplotrema increased. Haplotrema oviposits in June. Haplotrema behaved as might be expected except for 1940 (Fig. 12). There were no records of specimens taken of this species within that year. Its entire population may have retreated to logs, which are not sampled and which are important places for the regular abode of this species.

Most species decreased in correlation with low spring rainfall of 1946; Carychium and Deroceras were unexplainable exceptions. High dry spots are regularly used for making collections and Mr. G. Webb states that Carychium aggregates in moist spots. It is likely that Deroceras behaved similarly. Why did Retinella (Fig. 12) increase in 1941 and Vertigo and Collumella decline The only possible suggestion is in Fig. 10; 1941 was a favorable year as to spring rainfall, but there was an extreme drought in July. This would leave opportunity for differential destruction of individuals of different species with life histories which differed in the date of sensitive periods. However, it is equally probable that the differences in numbers are not significant because of small population and species habits and irregular distribution affecting numbers collected.

After 1943 there were many peculiar variations of the population of different species wtih sharp contrasts as to totals. Fig. 10 and the climographs in Fig. 11 show also erratic month-to-month changes in temperature and rainfall. The year 1944 was generally favorable to the Trelease Woods mollusks.

There was much rain and there were no dry periods of significance during late spring and early summer; the dry periods of late summer and autumn were short and evenly spaced. The population response among mollusks followed a general pattern of increase. It is quite possible that there can be too much rain for some species; for example Succinea, the population of which remained nearly static from 1936 to 1938. However, its habits indicate that it may frequently be missed in routine collections.

The long and rather evenly spaced dry periods in 1946 (Fig. 10) may be credited with causing the decreases shown in the total population. The difference in population variations between species must await fuller knowledge of sensitive periods in life histories and better records of conditions.

C. FOREST INSECTS AND MISCELLANEOUS ARTHROPODS

This group, as might be expected, presented the greatest differences between species as evidenced by the diversity of habits and the portion of the habitat occupied. It has proved impracticable so far to present accounts restricted to any taxonomic groups except the mollusks and millipeds.

A considerable number of species do not follow the general trends and correlations with weather already indicated for many others. To illustrate what

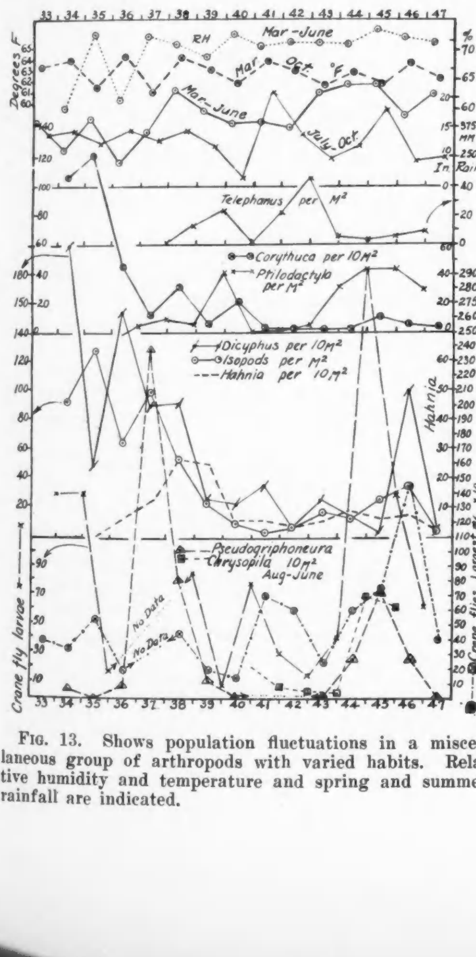

FIG. 13. Shows population fluctuations in a miscellaneous group of arthropods with varied habits. Relative humidity and temperature and spring and summer rainfall are indicated.

appears to be irregular types, Fig. 13 was drawn to include two species which live on the vegetation and which do not follow the trends of the herb-shrub spiders and the species and categories shown in Figs. 9 and 12. Included are the flat bark beetle, *Telephanus velox* Hold, which lives more often in litter than under bark; species living in and on the litter throughout their life histories, e.g., the isopods and the ground spider (Hahnia); leaf-feeding Hemiptera, *Corythucha aseculi* O & D and *Dicyphus gracilentus* Parsh., with peculiar population distributions; and forms with larvae inhabiting the soil or litter, which includes all the Diptera and the beetle, *Ptilodactyla serricollis* (Say).

Of the species censused in the larval stage, the crane flies (Diptera) are outstanding in abundance and number of species. Concerning the adults of these, Rogers (1933, p. 29) has said:

"Although definite knowledge of the duration of the life of adults in nature is difficult to obtain, observations on specimens in breeding cages, as well as repeated field notes on emergence and disappearance within isolated habitats, indicate that few of the smaller Limoniinae live longer than two weeks and few of the Tipulinae attain an age of three weeks. For many species, and the huge majority of individuals of all species, adult existence is far shorter than these estimated maxima. Barring interruption due to low temperatures or occasional periods of widely prevalent low humidity, the essential adult functions of mating and oviposition are completed within two-four days of emergence."

Accurate determination of size of populations of crane flies and some other species is seriously affected by too infrequent collections. It would appear that, for the adult tipulid population, collections should be made on alternate days. Inspection of the records led to the belief that the largest collection of adults in each year was useful (Fig. 7) as the basis for a population index. The largest combined herb-shrub collection for each year was divided by two and multiplied by 10 to give an index of the largest number per 10 m². This resulting index number was greatest in 1946, following increases in 1944 and 1945, which has been true of several categories. The tipulid larvae are easily recognized as to the family. Fig. 13 shows the abundance of larvae based on August through June collections plotted on the space between the years. J. Speed Rogers stated in connection with his identification of the larvae that *Tipula duplex* Walk. made up approximately half of the larvae; Chrysopila is abundant but less numerous than *Tipula duplex* Walk. There is a separate graph of the population of Chrysopila larvae (Fig. 13) 1941-46. This follows the trend of the total larvae except in 1943, plotted in the space between 1943 and 1944. The difference in 1943 probably indicates a physiological difference between Chrysopila and the more abundant species which make up the total. The initial years (1934, 1935) had a large total population of larvae although they were dry years suitable for non-forest

species. Because of missing collections in 1934-38, this period cannot be interpreted. The larvae increased with the increase in spring rainfall of 1943 and 1944 but declined in 1945. They were abundant in the fall and winter of 1944-45 and 1945-46. The adults were abundant in the summer following the years of abundant larvae, but in 1945 the number of adults was not proportional to the number of preceding larvae. The long autumn drought (Fig. 10) in 1946, extending to Oct. 23, followed by a winter and spring drought covering February, and the first half of March was followed by general population declines.

As to other Diptera, the records show *Sympycnus lineatus* Loew, *Homoneura inserta* (Mall.), *Thamatomyia glabra* (Meig.), and *Minnuetia lupulina* (F.) are good for quantitative studies, but regular collections are too few to constitute good samples much of the time and identification difficulties caused gaps in the records. *Pseudogriphoneura crevecoeuri* is an example of a fly that is present over a long enough period to make fortnightly collections effective. Its population indices are shown in Fig. 13. Its population was unusually high in 1937 and moderately high in 1945. It dropped to lows in 1940, 1943, and 1947. Late summer drought periods in 1939 and 1946, with February-March added (Fig. 10), may account for 1940 and 1946 declines but 1943 is not clearly the same. It is not clear as to why the population dropped almost to zero in 1947. June rainfall was very heavy, and water stood in part of the woods for many days.

Hahnia, the only strictly litter-inhabiting spider coming in our collections regularly, had the largest population of the 14-year period in 1937. The populations in other years were too small to show significant differences from year to year.

The isopod population declined in general in 1936, 1938 to 1941, inclusive, and 1947 (Fig. 13). Other years in this 1933-1947 period showed increases. except 1944, in which the population remained static. The decreases were found to occur in conjunction with heavy June rainfall followed by a dry July in the years showing decreases, except 1936, with a dry period covering May to August. Increases in general appeared to be favored by abundant rainfall in April and May, but when the rainfall continued through June, decreases resulted; none of these suggestions are fully consistent, however.

The lacebug (*Corythuca aesculi* O & D), the mirid (*Dicyphus gracilentus* Parsh.) Fig. 13, and the basswood beetle (*Baliosus rubrer* (Web.)) (not shown on graph) show what may be pseudo-evidence of being favored by lowered rainfall and thus resembling the non-forest species. Stehr (1938), who made a study of Corythuca, stated that it hibernates under bark of standing trees and in places not easily found. He added that winter collections give no indication of the size of the population but failed to state whether his studies were made in virgin forest or disturbed pastured woods without normal litter. We made no tree trunk collections, and only five winter forest-floor specimens were taken in more than 160 soil-litter collections, December through March 1933-1947. It is inferred that in dry periods the population moves to the lower available buckeye leaves where the atmospheric moisture is greater than nearer the tree tops. The size of the collection is clearly related to such an hypothesis, particularly in the breeding period (Fig. 13). This explanation applies also to *Baliosus ruber*, the basswood beetle. Both the species showed large populations in 1934 and 1936. Baliosus showed another high in 1944, not duplicated by Corythuca.

Dicyphus overwinters in the adult stage and appears to be favored by high March-October temperature and low spring rainfall (Fig. 13). The presence of drought periods in the second half of May of 1934, 1936, and 1946 which accompany the largest populations shown in Fig. 10, indicates that this is one of the critical periods in the development of Dicyphus. The largest population accompanied a dry period in April and the first half of May and rain in the last half of May with temperatures 6.3° F. above normal in 1934. Dicyphus rose to another high level in 1936 with a dry April and wet May with temperature 4.3° F. above normal. It rose from a very low population in 1945 to a small maximum in 1946 with April dry and 4.2° F. above normal but with an excess of rain in May. It declined again in 1947 but became exceptionally abundant in 1949 (personal communication of M. B. Eyster), with conditions roughly similiar to those of 1934. The decreases are less easy to explain than the increases. An inspection of Fig. 10 suggests that July droughts may be detrimental to nymphs, as such droughts were accompanied by decreases. Heavy rains may also be detrimental to young nymphs of these and other small Hemiptera. Until more details are known as to the life history, there will be difficulty in explaining the weather relations.

Ptilodactyla larvae were the most abundant beetle larvae, giving an index of nearly 100 per m^2 in 1939-40, 1944-45, and 1945-46. As many as 70 have been taken on $1/10$ m^2 (Sept. 4, 1939). The adult beetles appear in June and early July. Fig. 13 shows the larval populations based on August through June totals divided by the number of months with actual collections of larvae. It appears to give a fair expression of relative abundance for cases in which the organisms appear to be spotted in distribution. The abundance of the larvae increased sharply in the 1939-1940 and 1943-1944 periods. The trend of this population does not coincide with the population trend of other litter inhabiting species. A rainy June in 1939 and a rainy May in 1943 followed by a late dry summer and autumn (Fig. 10, 1939 and 1943) may have offered the most favorable conditions.

Telephanus velox Hald. is unusual because it increased in 1938, 1939, 1941, and 1942 when nearly every other species declined. Few correlations of this insect with weather can be pointed out. The 1941 and 1942 increases have nothing in common except heavy June rainfall followed by drought, which is

equally characteristic of 1939 and 1940. The years 1939 and 1940 had late summer droughts and 1941 and 1942 did not and the increase was greater. Summer droughts characterized all the remaining low population years and were less intense in 1945 and 1946 (see Seamans 1926).

D. ANIMALS SPENDING COMPLETE LIFE HISTORIES OUTSIDE THE SHELTER OF LITTER

It is desirable to check the relations of animals which spend entire life histories in the herbs or shrubs subject to the atmospheric conditions above the soil. The tree crickets and several spiders definitely have such relations. Some of the spiders which have been censused are unfortunately not well known as to life histories. *Micrathena gracilis* (Walck.) is nearest to the tree cricket Oecanthus in general location, both being at a relatively high level in winter.

Mangora gibberosa Hentz and some *M. maculata* Keys. have been followed throughout the period of study. The two cannot be separated when immature and there was some past difficulty with the adults. The vast majority of individuals of this genus are *M. gibberosa*. Weese (1924) collected egg sacks in the fall and winter and studied the effect of temperature and humidity on their development and on the development of the egg parasites. He studied reactions in vertical gradients of light, evaporating power of air, temperature, etc. The average height of the spider above the ground is 0.7 m and presumably the egg sacks were at a similar level. In his study, Weese included Anyphaena (the young of which are found at the 1.25 m level) and Micrathena, as well as *M. gibberosa*. The egg sacks of the last two are fully exposed during the winter. The young emerge in spring and mature in early summer. This condition is probable for the other species considered. The time of appearance of mature specimens is as follows: *Anyphaena pectorosa* (Koch), April and later; *Dictyna foliacea* (Hentz), May and later; *Zygoballus bettini* (Peck), August 1 and later; *Mangora gibberosa* (Hentz), late July and later; *Mangora maculata* (Koch), early July and later.

The tree crickets, Oecanthus, are probably represented in the woods by *O. angustipennis* Fitch, and occasionally by other species, which cannot be differentiated in the young stages. They deposit their eggs in twigs of shrubs and tree seedlings in the autumn, thus exposing them to the atmospheric conditions throughout the winter. Fig. 16 herein, and Fig. 3 of Shelford (1951), when compared with Fig. 14, will show the relations of individual species to the total herb-shrub spiders and also the rough agreement with the soil and litter inhabiting forms noted. The herb-shrub spiders have been discussed briefly in their relation to other maxima and the solar phenomena shown (Shelford 1951). The main features of this spider curve agree roughly with those of the ground inhabiting species shown in Fig. 8, with maxima in 1937 and 1945-47. There is only a similarity between population trends of spiders and millipeds from 1934 to 1937. Millipeds increased in 1938 and spiders decreased and continued to decline to a low in 1940 and increased slightly from 1939 through 1943, sharply in 1944 to a maximum in 1946 and declined in 1947. The maximum in 1946 and decline in 1947 is a difference from most other groups and species except two or more species indicated in Figure 13.

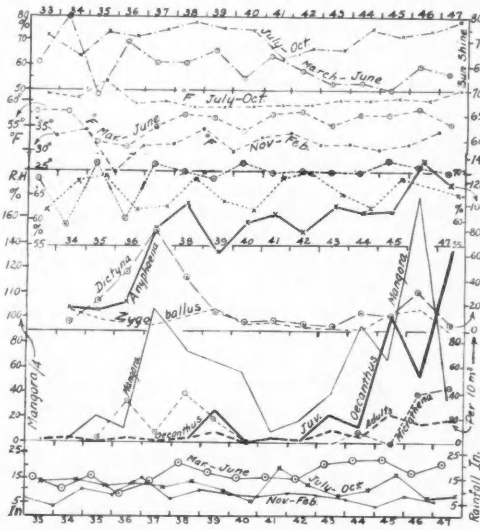

FIG. 14. Shows the fluctuations in populations of seven species of insects and spiders which are exposed to the atmosphere throughout the winter period. The winter temperature and rainfall are shown, but no correlations with low winter temperatures are evident.

Graphs of population indices of three species are shown near the center of Figure 14. In the lower part of the figure, Oecanthus and Micrathena are on the same scale, but it was necessary to use the Mangora index figure divided by four.

The population of *Zygoballus bettini* was smallest and sampling therefore was less reliable, but slight increases were apparent in 1939 and 1946-47. *Anyphaena pectorosa* shows a small population, probably due to the drought conditions, in 1934 but a high in 1938. The population remained at a high level throughout 1939 to 1945, when it went to unusually high levels. *Dictyna foliacea* followed the usual variations with high populations in 1937 and 1946. Anyphaena and Zygoballus populations are in agreement with the total herb-shrub spider population (Fig. 16) as the 1934 population is greater than that of 1935. The population of no one species agrees with the total herb-shrub spider population in detail; Mangora approaches nearest but was more abundant in 1935 than in 1936 and declined in 1945. The reverse was the case for Micrathena, the highs for which were in 1936, 1938, and 1946-47. The Mangora populations declined in 1938 and 1947, in general agreement with the herb-shrub spider population. Nevertheless, the sum of all the populations

shown in Fig. 14 is in general agreement with population of litter-inhabiting species (Fig. 8). The five species presented here are supplemented in the woods by eight listed as abundant by Jones (1946), and a score of less common and incidental, and immature ones which are included in the herb-shrub population graphed with maxima in 1937 and 1946.

Figure 14 has been prepared to check these animals which have fully exposed life histories. It is evident that high spring rainfall is favorable. The generally low population at the end of the 1933-1934 dry period appears to indicate the importance of rainfall to the larger fluctuation. Attention will first be focused on the factors not discussed in detail in other cases. The winter of 1935-36 was severe. There were 19 days with 0° F. or below during January and February, 1936; these months showed −5.7° and −9.7° departure from normal, respectively. An increase of considerable magnitude in the populations of all excepting Mangora and possibly Zygoballus followed this severe winter. In 1940 the temperature for January (Fig. 11, '40) showed a monthly mean of 14.2° F. or −10° C. Eleven days were 0° F. (or −17.7° C.) or lower. A decrease of all except Anyphaena followed this severe winter. The correlations are practically reversed for the two winters. The 1940 declines may have resulted from fall, winter, or spring dry periods; the 1936 rainfall differed in distribution. The low temperature winter of 1944-45 (mean of Dec. and Jan., 16° F.), which was accompanied by little rain, was followed by population decreases for some of the species; Oecanthus and Zygoballus increased. With this one exception (Zygoballus) the spider populations behaved in 1944 and 1945 like the centipeds (Fig. 8). There appears to be no important response to low winter temperatures.

The summer sunshine was high in 1937, 1938, and 1939, the period of general spider high populations or increases. Correlations with relative humidity of the atmosphere outside the woods were fairly good for the high populations, but the July-October humidity was high when the populations were lowest. The increase followed the spring rainfall and absence of dry periods better than any other factor with available records.

The Oecanthus indices for adults and nymphs are shown. The records show that nymphs were not recorded until 1938. The populations of adults were too small to be entirely reliable. No conclusions are possible relative to the apparent lack of an Oecanthus increase in 1937, but the later populations follow the general rules.

E. SPECIES WITHOUT DETERMINABLE YEAR-TO-YEAR GENERATIONS

The ants may be characterized in a manner indicated by the heading. Three graphs of population are presented in Fig. 15, representing herb-shrub total, the population of *Leptothorax curvispinosus* Mayr, a species taken almost exclusively from herbs and shrubs, and *Aphenogaster fulva aquia* (Buck), taken from the soil. It will be recalled that we omitted soil ants from soil collections because of assumed irregular distribution. In this case, collections of more than 110 specimens per sq. meter were assumed to be near a nest and were omitted from the curve and the others treated as if these collections had not been made. There were two such collections in 1938, and one each in 1940, 1945, and 1946.

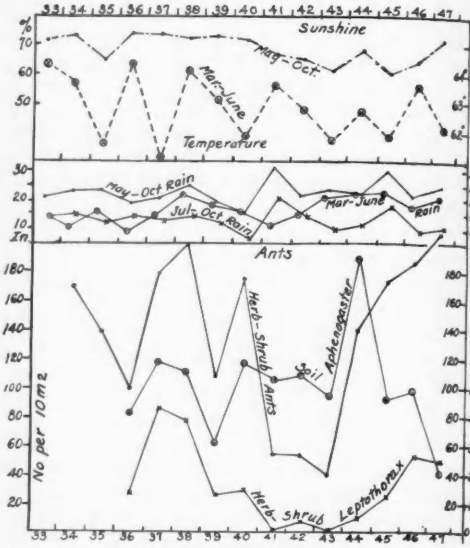

FIG. 15. Shows the fluctuations in populations of ants divided into those taken from the herbs and shrubs and those from the soil. The sunshine from May to October when the ants are active is shown because it was thought to be a possible factor in the number of ants obtained from the herbs and shrubs, but no correlation is shown. The sharp increase in 1940, the driest year of the study period, is unexplained. The decline of the soil species in 1945 came when the annual rainfall was 48.01 in. and more than 9 in. above normal.

The trends of three graphs show considerable similarity 1936 through 1944. All showed sharp rises for 1937. Curves representing the two separated species declined slightly for 1938 but the herb-shrub aggregate population increased considerably. All declined sharply in 1939. All increased in varying amounts in 1940, and subsequent changes were in the same direction to and including 1944. Thereafter, Aphenogaster, the soil species, deviated sharply from the herb and shrub combined population and Leptothorax, by declining to a very low figure, while the herb and shrub inhabitants increased. Leptothorax colonies are usually in logs and evidently the other herb-shrub species are also. The prolonged increasing annual and spring rainfall evidently reduced the Aphenogaster.

The graph suggests that the relation is to soil and log moisture rather than directly to the amount of precipitation. Soil moisture data are not available. It does not appear possible to explain the large number of specimens taken at the end of the dry period

of 1934. In 1935 the collections were heaviest following the rains which Rice states broke the drought. The sunshine for May through October does not afford any correlations that would lead to the assumption that more light brought more ants onto the herbs and shrubs to be caught. The relation to summer and open season temperature or any of the three long period rainfall graphs are contradictory. The extreme cold of the winter of 1935-36 may have been detrimental; however, no extreme cold occurred in the winter of 1938-39.

Leptothorax follows the general rule of most of the forest populations. It is rarely taken in the ground collections. The maximum in 1946 appears to follow increases which almost doubled with each year from 1944 to 1946, inclusive, and may be due to slow increases of the size of colonies each year under moderately favorable conditions. A comparison of peak populations shows 1936-1937 with a larger rate of increase (3.5 times) than 1944-1945. The most striking difference (Figs. 10, 11) lies in the preceding autumns: 1936, wet, no dry periods in September and October; 1944, dry periods in both. The April, May, and June total rainfall is similar in the two years.

F. TOTAL INVERTEBRATE POPULATION

The population is shown by months July, 1941, through October, 1947, in Figure 2. Its difference from the non-forest population is shown in Fig. 16, with the ground and herb-shrub populations separated, and in Shelford 1951, Fig. 4, where the ground and foliage populations are combined. There was a peak in 1937-38 and again in 1945-47, with two or three years of somewhat smaller populations associated with these dates. In Figure 16 the June-August sums of monthly means are used as more nearly expressing the value of the new generation of any year than the May-October value used by Shelford (1951), because by June many overwintering adults would have deposited eggs and died, especially in the case of foliage inhabitants. The herb-shrub values parallel the grand total on the six-month basis except for 1938 and 1939 where there are minor differences. The high 1939 value in Shelford (1951) is due to unusually large soil collections in September and October not included in Figure 16.

Smith (1929, 1930) data are good evidence that 1926 came in another high period. The May through October indices per m² for 1926 are estimated as 1,400; for 1936, 337; 1937, 659; 1938, 573; 1939, 594; 1945, 1,425; 1946, 1,486; and 1947, 1,700. The lowest index is 280 for 1942. These months include all species at their maximum availability for sampling. The 1939 population index is discordant with those treated ~~in detail in Figures~~ 3, 8, 12, 13, 14, ~~and~~ 15. Only a few of the species treated show large populations or increase in 1939. In that year there were, however, among other things large numbers of adult staphylinids and their larvae and very large numbers of larvae of *Ptilodactyla serricollus* Say, though very few adults were taken. There is also

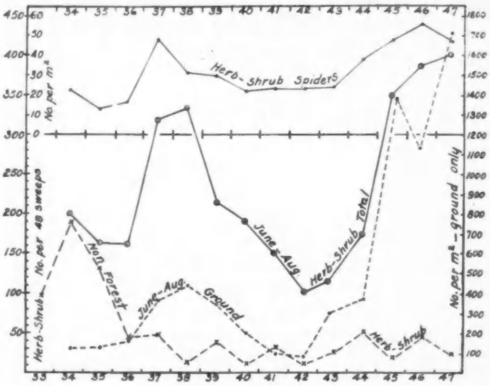

FIG. 16. The herb-shrub spiders of Trelease Woods as the average of the monthly means May through October per m². The herb-shrub woods population, 1934 through 1947, as the average of June, July, and August monthly means per 48 sweeps. Note large increases in 1937 and in 1945.

The non-forest population August through June per m². Note 1942 lowest of both forest and non-forest populations. The combined soil and litter populations (right hand scale 200-1800). Note mean of a little more than 200, 1934 to 1944, then an increase from 364 to 1378 in 1945.

some evidence that fly populations were unusually large, especially those whose larvae live in litter. The populations of all the litter-inhabiting species were very low during the drought of 1933-1936; they evidently built up during 1937 and 1938, and carried over into 1939 with an increase. The discrepancies among the individual species are not surprising when it is considered that only about 10 percent of the species received separate study and only a part of these are discussed.

Figure 17 shows the limits of 10-day climographs for years of population increase. A dry period of 10 or more days suggested by the deep indentation of the figure for forest populations may be significant. The limits contrast with the limits of 10-day temperature and rainfall of the non-forest species. For large non-forest populations the notch represents three 10-day dry periods and is very large. The rainfall is lower and temperatures are higher than for large forest populations (Shelford & Flint 1943).

With rather heavy rain it is surprising that the invertebrate population index for 1941 and 1942 fell to a lower point than during the drought period (1936; 337 per m²). The 1941 index was only 87% of that of 1936, and 1942 only 83% of that of 1936.

There was a large population decrease in 1940 (from 594 to 455 per m²). The 10-day climograph is peculiar (Fig. 17) in that there are no single 10-day dry periods; each 10 days is at or near 1 in. of rain. The total April, May, and June rain was 13.53 in. (normal 11.16 in.), and April-May 8.49 (normal 7.42 in.). In the year of maximum, 1937, April-May rain was 7.97 in. (April, May, June rain 13.30 in., Fig. 15B) while the other years of sharp

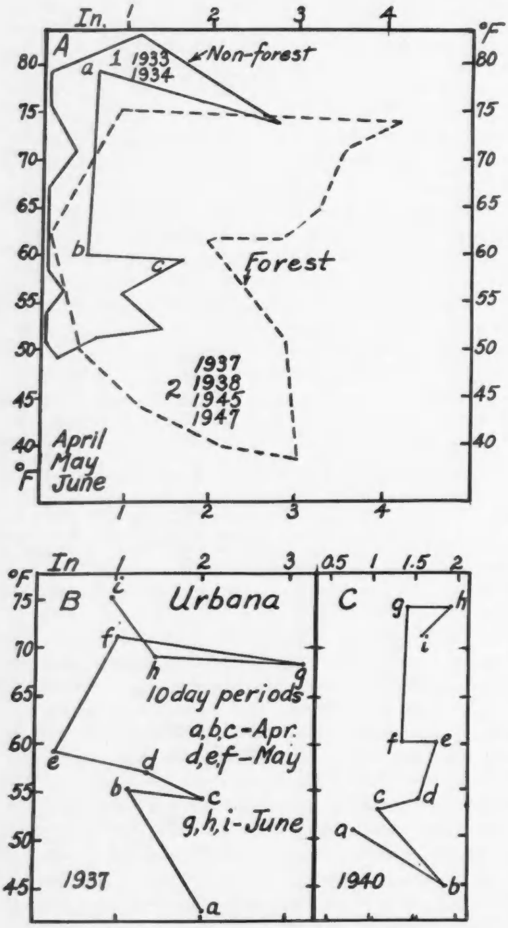

FIG. 17. A. The climographs showing the limits of temperature and rainfall for (1) a two year period of high non-forest population (1933-1934, solid line) and (2) the years of high forest populations (1937, 1938, 1945, 1947, dotted line). The notches representing dry periods and points representing high rainfall appear to be important. The difference in total rainfall and temperature favorable to the two groups is noteworthy.

B. The 10-day climograph of the year 1937, which was especially favorable to forest populations. The letters a, b, and c represent the three 10-day periods of April; d, e, and f of May; and g, h, and i of June.

C. The 10-day climograph of the year 1940, the driest of the 14 years of study; yet rain was almost continuous in April, May, and June, and populations of both forest and non-forest species declined.

increase were above 9.46 in. or more. There appears to be nothing in the years 1940 and 1941 from the standpoint of temperature, or rainfall, either in amount or distribution, which differs from years of higher population (Fig. 15). The correlation of these low populations is probably with a solar radiation factor discussed on later pages.

V. FOREST VERTEBRATES

These have received the attention of my colleagues. The squirrel studies began too late to afford much opportunity for year to year comparison. Records of foxes, opossums, and raccoons are scattered and began late. Mouse population studies carried on by Dr. Kendeigh have not been prepared for publication. Several forest bird populations have been published by Kendeigh (1944, 1948). The white-breasted nuthatch, tufted titmouse, and downy woodpecker were censused 1926-29, 1933-35, and 1937 to 1948. In general the maxima after summer reproduction for these birds, as shown by autumn-winter counts (Shelford 1951) do not agree with those of the invertebrates. The maximum in the 1934-37 period is not clear because of missing data for 1936, but the second maximum of the period came in 1942 when all invertebrates, both forest and non-forest, were at an extreme low of the period.

The house wren was represented by a single pair in 1927 at Trelease Woods. Wrens increased quite regularly from 1934, when 3 pairs were present, to 40 pairs in 1940 and, following a decline, rose to 45 in 1947. The year 1940 was the driest of the 14 years of the Trelease Woods study period. The Trelease wren population agrees roughly with that of the resident birds. There is no evidence that a direct relationship to rainfall exists, but the invasion of Trelease Woods by increasing numbers of house wrens has accompanied a general upward trend in rainfall in eastern U. S. A., 1934 to 1947. The highest percentage summer increase in Kendeigh's (1944) 1925-1934 house wren population near Cleveland, O., was in 1925 and in 1929.

As to mammals, the woodland deer mouse, *Peromyscus leucopus noreboracensis* (Fischer), showed a large population in 1937-38 in Trelease Woods (Lindeborg 1941). Shanks (1946) points out a sharp inrease in 1936 with a large maximum in 1937 for the opossum in Illinois and a similar but lesser 1937 peak for raccoons and red foxes, and he concludes that the critical months were January through April (see Errington 1945, p. 7; Lindeborg 1941).

VI. GENERAL POPULATIONS IN RELATION TO SOLAR RADIATION AND RAINFALL

There is evidence that forest species are influenced probably directly by ultraviolet or other shorter wave radiation. A decrease in forest population such as that in 1941 appears not to be correlated with any other factors. The Trelease Woods studies overlap the ultraviolet record of Pettit (I.A.U. 1924-1938), Luckiesh (1946) for the years 1935-1941 with 1939 omitted, and Coblentz (1945) for the years 1941-1944. The Pettit ratios give a rough astronomical value which tends to average about the same from month to month in midsummer of a particular year, while the actual values to which organisms are exposed vary with the length of the atmospheric path and transparency of the atmosphere, especially the amount of atmospheric water vapor (Shelford

1951). Luckiesh (1946) gives his measurements in sums of E-vitons which, divided by 2.5, give milliwatts min/cm^2 which were used by Coblentz (1945). Their summations for 1941 differ; the Luckiesh data are only 17.6% of the Coblentz data, probably due to differences in wave lengths measured (Shelford 1951).

There have been a few studies of the solar radiation penetrating the forest canopy. Shelford (1929, p. 318), using six screened phototubes, found the greatest transmission through the broad-leafed forest canopy of Trelease Woods in midsummer of 1926 to be about 10% at 570 mμ in the yellow. It decreased sharply to 2% at 520 mμ and continued nearly the same into the ultraviolet. In some readings there was a slight increase toward the shortwave up to 7%. The readings in the ultraviolet were about the same as in the blue and violet but occasionally a little higher.

Strohecker (1938), using a caesium oxide phototube, showed averages varying from 1 to 12% of the total ultraviolet in sun flecks in a climax beech-maple forest. The Trelease Woods is a subclimax red oak-maple forest with a similar canopy. Atkins, Poole, & Stanbury (1937) studied light intensity and color in woods in Britain. There are other studies reviewed by Strohecker (1938).

The relations of invertebrates to ultraviolet as a reproductive stimulus is best studied in species which breed in the spring and whose resulting new generations can be segregated in the sampling later in the summer. Both Dicyphus and Anoplitis appear to meet these requirements but for the fact that Dicyphus is present in very small numbers in winter and spring, which may mean that some individuals deposit eggs in the autumn. The mean of the two highest collections of two consecutive months were used as indicators of the new generation population. Ultraviolet-hydrograms were attempted for both species. Neither April nor May ultraviolet, in combination with rainfall or relative humidity, yielded good results. With May ultraviolet both were somewhat contradictory. With April ultraviolet Dicyphus yielded a fair hydrogram, with an irregularity but no contradictions. April light conditions appear more important than those of May. Anoplitis diagrams were less regular than those for Dicyphus. It appears that Anoplitis is more responsive to May ultraviolet than to April.

The fox, raccoon, and opossum (Shanks 1946) did not show ultraviolet hydrograms in a few attempts to develop them. But in all these cases the ultraviolet data are broken betwen three different records and good results cannot be expected in the case of these mammals with the small number of items and the 1931, 1932, 1933, and 1942 population data missing. Furthermore, these mammals are nocturnal and a response to solar radiation, if it occurs, is to be expected through food supply which originated the year before breeding.

The only wood species of bird with a consistent record covering a considerable number of years of summer increase in population is the migratory house wren. There are ten years of wren data for near Cleveland, O. (Kendeigh 1941), ending with 1934 within the Pettit record of ultraviolet intensity on Mount Wilson, which serves as a sort of world-wide general measure of relative intensity.

Kendeigh's (1944) published data were reworked by Errington (1945) and the percent increase in population was calcuated from Errington's data, 1925 through 1934. The annual percent increase over this period suggests the type of ultraviolet-hydrogram shown in Figure 18A. Forest species evidently are governed by the same principles with regard to solar radiation as the non-forest (see Seibert 1949).

Figure 18B shows the ultraviolet and rainfall for the spring and early summer months of 1937 (a good year for forest animals) and 1934 (an excellent year for non-forest species). The greater ultraviolet intensity and rainfall in 1937 are evident. Figure 18C shows the relationships of invertebrate populations. The high populations are probably largely determined by some factor operating chiefly in April. It will be noted that the only forest large population coming within the period in which the ultraviolet light intensity is known came in a year when April ultraviolet light intensity was about 128 (100 x Pettit's 1.28).

Smith-Davidson (1932), in addition to the 1926 figure for total population (1930), also showed that the Mangora populations per m^2 were much higher than in 1946, both in 1925 and 1926. Thus for large populations or large increases in population, the April ultraviolet ratio would be at approximately 128.5 or above (1925 April ratio was 129). The Aprils of years of high populations and large increases fall within the smaller ellipse of Figure 18A between ultraviolet 115 and 128 or 129. The Luckiesh scale on the right is in erythermal units for the years divided by 100 and merely indicates a high record for 1940 and 1941. If the unmodified April-May ultraviolet or Pettit, Luckiesh, and Coblentz is drawn, for example, above the populations of the foliage in Fig. 18, as was done in Fig. 9 of Shelford (1951) with an optimum limit, it would suggest that all decreases had occurred when ultraviolet was either much too low or much too high, except in 1944. This figure is not presented, because some of the adults and late immature stages which make up the population would have had to be stimulated in adult stages of the autumn before, if stimulation of the adult is necessary. In any case the population is very heterogeneous as to time and place of stimulation and even more heterogeneous as to time of sensitive periods. It is probably significant that Fig. 9 (Shelford 1951) could be duplicated with the exception of 1944 when the optimum is placed between 111 and 131, the April-May mean on the Pettit scale. 1944 had the highest spring rainfall of any year in the applicable ultraviolet record period (1933-1944). In

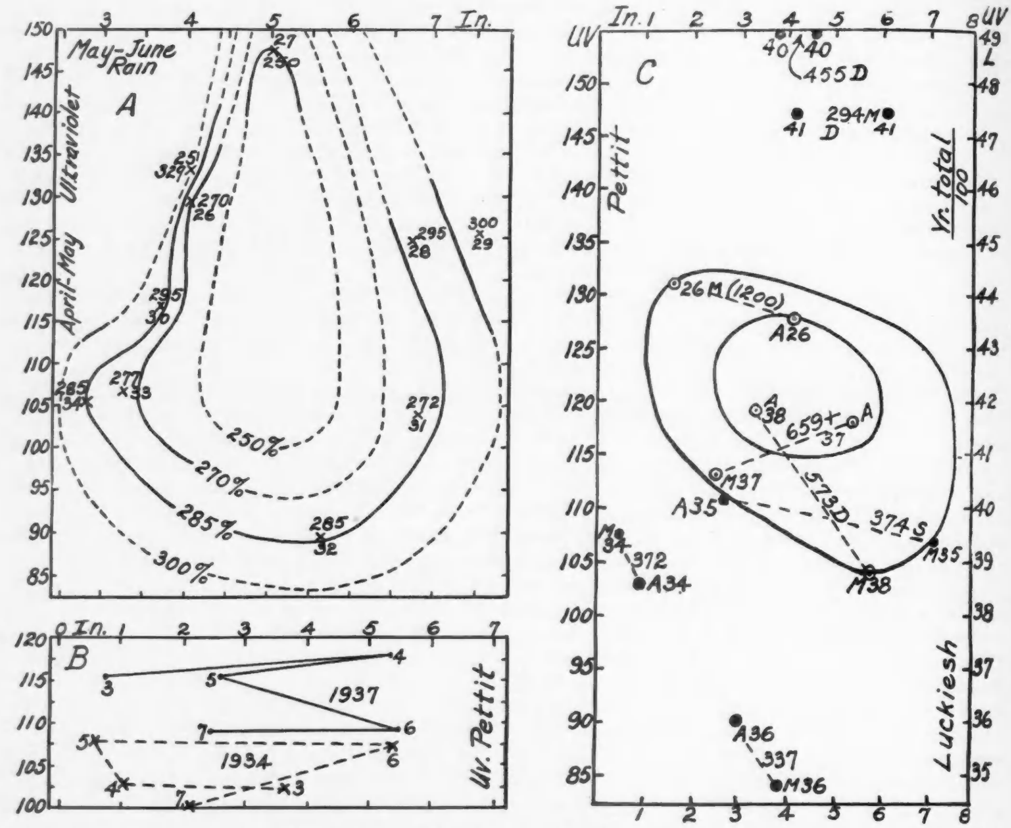

FIG. 18. A suggested ultraviolet-hydrogram for the percentage increase of the house wren near Cleveland, Ohio. 1925 through 1934. Calculated from Errington's (1945) tabulation of data from Kendeigh (1944).

B. Shows an ultraviolet-rainfall climograph for 1937 when forest invertebrates were at a maximum and 1934 when they were at a minimum and the non-forest species were at a high population level.

C. Shows limits of years with large forest populations. Open circles indicate large populations, solid dots, small populations. The elliptical figures show the limits of April ultraviolet used in combination with April rainfall to give one coordinate point and May ultraviolet light in combination with May rainfall to give the other one. The two are connected by a line. A indicates April; M indicates May. The figures on the line are population indices. The 1926 index is estimated from Smith-Davidson's data. The left hand scale is Pettit's ultraviolet scale and the right hand scale indicates Luckiesh's annual sums of minimal perceptible erythemal (MPE) doses or hours for the years 1940 and 1941. 3540 for 1936 is placed opposite the April-May mean on the Pettit scale and 1940 and 1941 are shown at the top. They are very high years. One MPE dose is 240,000 ergs sec. Such summations cannot be used in graphing both April and May data because of the large difference between them.

every year, except the very rainy 1944, declines in forest population were associated with very high or very low ultraviolet values. The year 1934 (Fig. 17) was the ideal year for most non-forest species; the forest population was at a midpoint between high and low values; it declined in 1935 and 1936, due probably to April droughts and possibly to low ultraviolet (Fig. 18C). 1937 was a year of sharp increase accompanying favorable ultraviolet. The 1938 population (figured on a six-month basis but not June-August) was lower than the 1937. This is ascribed to a dry period that was brought out by the 10-day analysis. April 9 through May 13 had only 0.9 in. of rain, which is not evident in the monthly averages (Fig. 10), and lower ultraviolet light. The so called optimum limits of ultraviolet are very indefinite, for all we have in the record is a rough expression of higher and lower year to year values. The subject of relations to solar radiation is fully discussed in another paper (Shelford 1951).

Every animal exercises a large and often critical control over its exposure to sunlight. The reactions of individuals to sunflecks should be studied (Park 1931). Study of behavior reactions to ultraviolet is important (Bertholf 1931).

VII. SUMMARY AND CONCLUSIONS

(1) Approximately 500 species of invertebrates have been collected from Trelease Woods and identified by specialists. About 40 of these have been considered in this report.

The study extends over two periods of extremely low forest populations, 1933-34 and 1941-42, and through one and into a second period of high forest population, 1937-38 and 1945-46-47.

(2) This study of invertebrate populations has demonstrated that the sampling is sufficiently reliable to demonstrate beyond doubt that populations fluctuate from two to ten fold or more between periods of favorable and unfavorable conditions.

(3) Correlated phenomena indicate that forest invertebrates have responded to rainfall or moisture conditions in the direction of larger populations when rainfall is large. The rainfall of late March, April, and May and short dry periods appear to be most important.

(4) There were no undoubted correlations between size and temperature in the aggregate populations. Some individual species increased when temperature was high. There were few or no correlations between populations of spiders and tree crickets, which have young stages fully exposed all winter, and low winter temperatures. When considered together, the limits and distribution of temperature and rainfall for successful reproduction of forest species differ from those of non-forest species (page 210).

(5) The correlations between population size and the intensity of solar ultraviolet suggest an importance second only to rainfall. It operates with reference to an optimum or to maximum and minimum limits of intensity toleration in certain months in which organisms are sensitive. The optimum intensity is greater for forest inhabitants than for non-forest inhabitants (Fig. 17, p. 210).

(6) Periods in which forest populations failed to increase under favorable conditions of rainfall and temperature are correlated with too high or too low ultraviolet light intensities (Fig. 18, p. 212).

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